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The Yezo scallop, or Japanese common scallop, *Mizuhopecten yessoensis* (Jay)

FOREWORD

At the present stage of biological development, it is very important to have summaries on concrete species, including their systematics, morphology and physiology, chorology, ecology and ethology, as well as the factors of anthropogenic pressure to which a species is subjected. In the foreword to V.S. Levin's monograph on the Far Eastern trepang (1982), A.V. Zhirmunsky notes that having all the data available on a certain animal in a single book is extremely useful both for the characterization of the species, and for the detection of the problems that have to be dealt with in future investigations.

This monograph is devoted to the species characterization of the Yezo scallop (or the Japanese common scallop), one of the major marine animals utilized and cultivated in the Far East. The monograph is based on the charts and diagrams developed by the Institute of Evolutionary Animal Morphology and Ecology of the USSR Academy of Sciences and the Institute of Marine Biology of the Far Eastern Science Centre of the USSR Academy of Sciences for the book "Species of Fauna of the USSR and Contiguous Countries". The authors that have contributed to the book "Yezo Scallop" include researchers of the Institute of Marine Biology of the Far Eastern Science Centre of the USSR Academy of Sciences (A.A. Varaksin, S.M. Dzyuba, G.A. Yevseyev, Z.Ye. Yevtushenko, V.Z. Kalashnikov, A.A. Karpenko, V.L. Kas'yanov, A.I. Kafanov, V.S. Levin, L.A. Pozdnyakova, S.K. Ponurovsky, A.V. Rybakov, A.V. Silina, L.N. Usheva), the Pacific Scientific Research Institute of Fishery and Oceanography (Ye.A. Belogrudov, Yu.E. Bregman, Yu.V. Kurochkin, L.A. Makarova, L.V. Mikulich, V.G. Myasnikov, Ye.M. Tsimbalyuk) and the Pacific Oceanological Institute of the Far Eastern Science Centre of the USSR Academy of Sciences (P.M. Zhadan, P.G. Semen'kov, N.N. Chekmasova, V.P. Chelomin), who specialize in different areas of scallop biology. The contribution of each researcher to this book is reflected in the table of contents.

It seemed at first that the data available on the biology of the Yezo scallop was very limited. However, we found that our fears were unfounded as we continued to work on the book. The researchers of the Institute of Marine Biology have provided fairly extensive data on the taxonomic status of the mollusk, its anatomy development and growth, its population density and biomass, etc. Data on the commercial use and processing of the mollusk and its diseases and parasities have been correlated by the scientists of TINRO (Pacific Ocean Scientific Research Institute of Fisheries and Oceanography). The sense organs have been described by researchers of the Pacific Oceanological Institute.

At the same time, not all the problems of the species' biology have been solved. The monograph does not include any data on the muscular, excretory and vascular systems, and not enough data is available on the physiology and biochemistry of the species. In order to cultivate the scallop, it is especially important to study the conditions under which high productivity can be attained. According to the observations of Japanese scientists and practical workers in 1928 and 1956, millions of scallops have colonized vast territories. These "natural explosions" which resulted in a colossal increase in scallop biomass cannot be explained satisfactorily to this day.

Regardless of this, the monograph on the whole gives us a many-sided picture of the biology of the Yezo scallop, which can be applied in research and the national economy.

P.A. Motavkin

INTRODUCTION

"The History of Aomori" (1704) is the first piece of literature in which the Yezo scallop is mentioned., though we know the scallop has been commercially exploited by man since prehistoric times. Archaeological research data indicate that, beginning with the Stone Age, the population of the coastal areas of the Far East has been using the scallop as a food, and the scallop shells as a material for crockery, ornaments and objects of cult rites (Krasnov et al., 1977).

The Japanese name for this mollusk, "hotategai", literally means shell with a raised sail. In one of the legends of the Tsugara clan (Aomori Prefecture) which for a long time had exclusive rights to the scallop, it is described how scallops, rising from the depths with an open upper shell resembling a sail, swiftly tear along in shoals over the surface of the waves with the help of the wind. A part of the population of northern Hokkaido still believes that the scallop swims like a sailboat.

The scientific discovery of the scallop coincided with an event of great importance to the destiny of the Japanese people. In 1852-1854, the ships of US naval officer Matthew Perry visited Japan and brought it out of its long isolation from the rest of the world. In Hokadate, some scallop shells fell into the hands of the Americans, who took them back home. In 1856, an American scientist (Jay, 1856) , because of a certain similarity between the irregularities on the valves of the shells and the teeth of a comb, named the mollusk *Pecten yessoensis* and recorded it as a new species.

The end of the Tokugave period is regarded in Japanese history as the beginning of an organized Yezo scallop industry. Approximately from 1823, the Yezo scallop, like other marine animals (trepang, cuttlefish, octopus, fish, etc), was one of the commodities exported to China, and an important source of income for the rulers of Japan.

Economic interests prompted the people to expand the scallop industry and establish scallop farms. The latter appeared more than 100 years ago on Hokkaida (Japan), and are currently being developed in Primorsky Krai (Maritime Territory of the USSR) as well. The pursuit to expand the breeding of scallops and a number of other bivalve mollusks is due to a number of reasons. Their meat has a good taste and very important biological properties, and contains valuable proteins and active lipids with an array of phospholipids and polyenic fatty acids known for their hypocholesterinemic properties. As natural food components, scallop lipids have certain advantages over medicinal preparations in the treatment of certain diseases, especially in the prevention of atherosclerosis. Dozens of dishes prepared with scallop meat are known to modern culinary art; they combine good taste with therapeutic properties, and normalize the blood cholesterol level when used on a regular basis (Shchepin, 1976).

Among the pectinids, the Yezo scallop has the largest mass, grows quickly, and reaches marketable size in 14-15 months when cultivated in cages. The breeding of scallops is a profitable undertaking, and its pays off in a very short time. Crushed scallop shells are used as a food supplement for domestic animals. In Japan, the valves of the shells are used to make ashtrays, flower vases and various ornaments, and they also serve as a baking dish for the scallop meat.

Biologically active substances can be extracted from some of the organs of the Yezo scallop. For example, at certain times of the year, the neural ganglia contain a significant amount of hormones which are capable of stimulating the growth, sexual maturation and fecundity of mammals. The use of scallop neurohormones in livestock breeding can be a promising venture. The gills, intestine and especially the gonad during sexual maturation synthesize prostaglandins which are now being extensively used in medical practice. Being an active filter-feeder, the scallop is capable of trapping these substances from the environment and accumulating them in its tissues.

The traditional methods of breeding scallops are based on the installation of devices for spatfall, the collection of the young scallops, and the cultivation of the latter in cages. The further industrialization of breeding methods calls for control over the reproduction of gametes, the basis of species reproduction. Methods that accelerate maturation of the gonads, for which temperature is a decisive factor, have been developed and tested. It takes from 2 weeks to 2 months to obtain full-value gametes under these conditions, i.e maturation is reduced 6—18-fold in comparison with maturation under natural conditions without detriment to the active life of the scallop. The extensive use of thermal stimulation of gametogenesis in mariculture will make it possible to increase the output of marketable scallops, will fill the requirements of the scallop breeders, and will create favourable conditions for the planning and success of this industry. It will become possible to utilize females and males from different populations and speed up the maturation of their reproductive system. This will unquestionably speed up the breeding of highly productive lines of the Yezo scallop for the national economy, and its pure lines for research purposes. Because of the latest achievements in studying the regulatory mechanisms of the reproductive system in the scallop, it has become possible to delay or stimulate spawning as required with the help of acetylcholine and serotonin or their functional analogues. By combining the traditional methods with new ones and having studied the ecology of the scallop, we will be able to set up maricultural establishments with a controlled continuous and closed cycle, egg—larva—mature individual—egg. Further research is required to solve this important economic problem.

1. TAXONOMIC STATUS

1.1. Systematics

In the literature, particularly the Soviet literature, the Yezo scallop (Fig. 1) is most commonly identified as *Patinopecten yessoensis* (Jay, 1856), but this is incorrect. The genus *Patinopecten* Dall, 1898, p. 695[1] was established by Dall (Dall, 1898, p. 695) as a section of the genus *Pecten* Müller, 1776 with the type species (first designation) *Pecten caurinus* Gould, 1850, p. 345. The latter is known from the Pliocene, and today inhabits the shelf (10-200 m depths) of British Columbia, Washington, Oregon and California, from 36 to 59° N. lat. (Bernard, 1983). In addition to the type species, the Neogene forms *P. coosensis* (Shumard, 1858), *P. haywardensis* Lutz, 1951, etc. form the group of typical American patinopectens.

MacNeil (1961) established the new subgenus *Patinopecten (Lituyapecten)* MacNeil, 1961, p. 227 with the type species (initial designation) *P. (L.) lituyaensis* MacNeil, 1961 from the Upper Miocene and/or Lower Pliocene deposits of the Lituya Bay area (Alaska). Together with the type species, the subgenus includes the Miocene and Pliocene species *P. (L.) dilleri* (Dall, 1901), *P.* (*L.*) *falorensis* MacNeil, 1961, etc. We also distinguish a unique group of split-ribbed patinopectens from the Pliocene deposits of California, *P. healeyi* Arnold, 1906 and *P. lohri* Hertlein, 1928 (Addicott, 1974). It may be necessary to establish a new subgenus for this group.

Kuroda (1932) was apparently the first one to use the generic name *Patinopecten* for the Yezo scallop, after which the name began to be used for morphologically similar fossil forms as well. At least 23 valid species are listed under the name *Patinopecten* mentioned in Masuda's compendium. At the same time, Masuda was the first to note that the American and Asian "patinopectens" differ considerably from each other in the radial ribbing, the structure of the auricles and mainly the pseudohinge apparatus. This resulted in the designation of a new genus for the Asian "*Patinopecten* ", namely

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[1] The synonym of this genus is *Blanckenhornia* Teppner, 1922 (Fossilium catalogus, 1 Animalia, 15, S. 87, 260) with the type species *Pecten oweni* Arnold, 1906=*Pecten lohri* Hertlein, 1928 (method of designating type species unknown).

Mizuhopecten Masuda, 1963, p. 151, with the type species (first designation) *Pecten yessoensis* Jay, 1856.

The true *Patinopecten* are distinguished from *Mizuhopecten* by smaller lateral auricles, of which the anterior one of the right valve has a deep byssal notch; by a smaller posterior auricle in comparison with the anterior auricle on the left valve; by well-defined prolate auricular crura, which are well-delineated in juveniles but wear smooth with age; by weakly developed lateral ridges; by the presence of a double distal tooth of the posterior auricular crus on the left valve and its clearly developed distal teeth; by a more flattened right valve; by flattened and angular radial ribs on the right valve and somewhat sharper ones on the left valve (the ribs are rounded on both the right and the left valves in "mizuhopectens", and a fine reticulum is often observed on the left valve); by narrower (or almost as wide as the ribs) intercostal intervals on the right valve. These differences are of a stable nature, and point to the morphological individualism of the American and Asian "patinopectens".

In his review on the pectinids of Japan, Masuda (1962), a prominent specialist on the Paleogene-Neogene pectinids of the North Pacific, examines the Asian "*Patinopecten* s.s." together with *Pecten* (*Fortipecten*) Yabe et Hatai, 1940, p. 149 and *Patinopecten (Kotorapecten)* Masuda, 1962, p. 216 within the genus *Patinopecten* Dall, 1898, which together with *Pecten* Müller, 1776 is included by him in the subfamily Pectininae "Lamarck, 1819". Akiyama published a review of the Japanese "*Patinopecten* " (Akiyama, 1962) slightly before Masuda (1962). He separates the genus *Patinopecten* into two subgenera, *Patinopecten* s.s. (to which he also assigns the American forms) and *Patinopecten (Masudapecten)* Akiyama, 1962, p. 107. Akiyama synonymizes the genus *Fortipecten* with *Patinopecten* s.s., maintaining that the type species of the genus, *Pecten takahashii* Yokoyama, 1930, is a descendant of *P. murayamai murayamai* (Yokoyama, 1926) (=*Mizuhopecten kimurai murayami*), which adapted to the conditions of the coastal lagoons and, because of this, acquired a highly thickened and convex shell. This point of view is not shared by anyone today.

Analyzing the question of the so-called "*Patinopecten* " from Japan, Masuda (1963) substantiates the necessity of establishing the new subfamily Fortipectininae Masuda, 1963, p. 149 to include the genera *Fortipecten, Mizuhopecten, Kotorapecten, Nipponopecten and Masudapecten* . A controversy resulted between Masuda and MacNeil (MacNeil, 1967); the latter's point of view appears unsubstantiated to us, if only because he practically disregards the structural characters of the pseudohinge apparatus (an important complex of characters in group systematics) in his taxonomic research of the Pectinidae. The confusion occurred when MacNeil suggested using the name Patinopectininae as the nomen nudum. In a compendium on bivalves and scaphopods of Japan, Habe (1971, p. 91) presents the subfamily Patinopectininae "Masuda, 1962" with a diagnosis (in Japanese), in which he includes the genus *Patinopecten* with the subgenera *Patinopecten* s.s., *Mizuhopecten* , *Yabepecten* Masuda, 1963, p. 149 and *Kotorapecten* , as well as the genus *Fortipecten*.. Therefore, according to the rules of zoological nomenclature, Habe becomes the author of the subfamily Patinopectininae Habe, 1977. The latter is formed by *Patinopecten* s.s., *Patinopecten* (*Lituyapecten*) and, possibly, *Vertipecten* Grant et Gale, 1931. Consequently, the Japanese (Asian) and American "*Patinopecten* " belong to two different subfamilies, *Mizuhopecten* to the Fortipectininae, and *Patinopecten* to the Patinopectininae.

Thus, the taxonomic status of the Yezo scallop can be described in the following manner.

CLASS BIVALVIA LINNE, 1758
Superorder Autobranchia Grobben, 1894
Order Pectinida H. Adams et A. Adams, 1857
Suborder Pectinina H. Adams et A. Adams, 1857

Superfamily Pectinoidea Rafinesque, 1815
Family Pectinidae Rafinesque, 1815
Subfamily Fortipectininae Masuda, 1963

Genus *Mizuhopecten* Masuda, 1963
Yezo scallop *Mizuhopecten yessoensis* (Jay, 1856)

Synonymy:

Pecten yessoensis Jay, 1856, p. 293, pl. 3, fig. 3, 4, pl. 4, fig. 1, 2; Schrenck, 1867, in: Reisen und Forschungen in Amur-Lande, v. 2, p. 484, pl. 20, fig. 1-4; Lischke, 1869, Japanische Meeres--Conchylien, v. 1, p. 165, pl. 10, fig. 3, 4; 1871, ibid., v. 2, p. 157, pl. 13; Küster, Kobelt, 1888, in: Martini und Chemnitz Syst. Conchylien--Cabinet. V. 7, sect. 2, p. 139, pl. 38, fig. 7; Yoshiwara, 1902, Zool. Mag. Tokyo, v. 14, p. 142, pl. 1, fig. 2a, b; Yokoyama, 1911, J. Geol. Soc. Tokyo, v. 18, No. 208, p. 2, pl. 1, fig. 13, 14; 1920, J. Coll. Sci. Imp. Univ. Tokyo, v. 36, No. 6, p. 159, pl. 13, fig. 14, 15; 1931, J. Fac. Sci. Imp. Univer. Tokyo, sect. 2, v. 3, No. 4, p. 195, pl. 11, fig. 9; Taki, 1951, in: Hirase, An Illustrated Handbook of Shells in Natural Colors from the Japanese Islands and Adjacent Territory, pl. 14, fig. 1;

Pecten brandtii Schrenck, 1862, Bull. Acad. Imp. Sci. St. Petersburg, v. 4, p. 411;

Pecten (*Patinopecten*) *yessoensis* : Kuroda, 1932, in: An Illustrated Catalogue of Japanese Shells, Venus, v. 1-5, append., p. 99, fig. 110; Kinoshita, Isahaya, 1934, Rept. Fish. Surv. Hokkaido Fish. Exp. St., No. 33, p. 14, pl. 11, fig. 77; Kubota, 1950, Cen. Res., No. 6, p. 95, pl. 8, fig. 50; Skarlato, 1960, Bivalves of the Far Eastern Seas of the USSR (Order Dysodonta), p. 115, fig. 58, pl. 14; Zhidkova et al., 1968, Atlas of Upper Miocene and Pliocene Mollusks of Sakhalin Is., p. 87, pl. 43, fig. 1.

Patinopecten yessoensis: Habe, 1951, Genera of Japanese Shells, Pelecypoda (1), p. 82, fig. 161; 1955, Publ. Akkeshi Mar. Biol. Sta., No. 4, p. 7, pl. 4, fig. 6; Yamamoto, Habe, 1958, Bull. Asamuchi Mar. Biol. Sta. Tohoku Univ., v. 9, No. 1, p. 15, pl. 5, fig. 9; Kira, 1959, Coloured Illustrations of the Shells of Japan, p. 125, pl. 49, fig. 16; Habe, 1960, Publ. Shirikishinai Mar. Sta. Biol. Inst. Hokkaido Gakugei Univ., No. 4, pl. 5, fig. 13; Kira, 1960, Coloured Illustrations of the Shells of Japan, p. 125, pl. 49, fig. 16; 1962, Shells of the Western Pacific in Colour, p. 141, pl. 50, fig. 16; Sawada, 1962, Mem. Muroran Inst. Tech., v. 4, No. 1, p. 75, pl. 3, fig. 5, pl. 7, fig. 10; Takayasu, 1962, Rept. Inst. Undergr. Resources Akita Univ., No. 27, pl. 1, fig. 13, a, b; Kaseno, Matsuura, 1965, Sci. Rept. Kanazawa Univer., v. 10, No. 1, pl. 10, fig. 1, pl. 11, fig. 1, pl. 12, fig. 1, pl. 13, fig. 1; Golikov, Skarlato, 1967, Tr. Zool. in-ta AN SSSR, v. 42, p. 96, pl. 8, fig. 3;

Patinopecten (*Patinopecten*) *yessoensis* : Akiyama, 1962, p. 41; Masuda, 1962, p. 213, pl. 26, fig. 5, 6;

Mizuhopecten yessoensis : Masuda, 1963, p. 151, pl. 23, fig. 4, 5; Iwai, 1965, Bull. Educ. Fac. Hirosaki Univ., No. 15, p. 30, pl. 15, fig. 13, pl. 16, fig. 2; Noda, 1973, Res. Bull. Saito Hoon Kai Mus., No. 42, p. 36, pl. 5, fig. 5; Sinelnikova, 1975, p. 42, pl. 4, fig. 3, a, b, pl. 7, fig. 1, a-e, 2, a, b; Ogasawara, 1977, Sci. Rept. Tohoku Univ. Ser. 2, v. 47, No. 2, p. 97, pl. 8, fig. 3, a, b, pl. 9, fig. 1; Sinelnikova et al., 1979, Tr. Geol. in-ta AN SSSR, v. 333, p. 32, pl. 11, fig. 9;

Patinopecten (*Mizuhopecten*) *yessoensis* : Habe, Ito, 1965, Shells of the World in Colour, v. 1, p. 120, pl. 39, fig. 3; Habe, Kosuge, 1967, The Standard Book of Japanese Shells Illustrated in Colour, p. 132, pl. 49, fig. 7; Habe, 1977, p. 91; Skarlato, 1981, Bivalves of the Temperate Latitudes of the Western Part of the Pacific Ocean, p. 268, photo 190.

The type material (syntypes) might be deposited at the American Museum of Natural History in New York.

The type locality is Hakodate, Hokkaido.

1.2. Paleogeography

The most primitive Fortipectininae belong to the genus *Mizuhopecten* which up to the present day consists of one species, the Yezo scallop. The early stages in the history of this genus are documented by the remains of *M. chichibuensis* (Kan-no, 1957), described from the Upper Oligocene sandstones of the Nenokami region of Kanto in SE Honshu. Their ancestors most likely belonged to the genus *Chlamys* Röding, 1798. In addition to certain morphological similarities, this is confirmed by a number of biological characters of the juvenile stages of *Chlamys* and *Mizuhopecten* (Akiyama, 1962).

A significant increase in the species diversity of the genus *Mizuhopecten* is observed from the beginning of the Neogene. For example, considerable development is undergone by *M . kimurai* (Yokoyama, 1926), which forms a number of vicarious subspecies in space and time. At this time, the area of the genus takes in almost all of the Japanese islands (with the exception of Hokkaido) and NE Korea.

In the Early Miocene, there was intensive divergence of the Fortipectininae, which resulted in the formation of *Kotorapecten*, *Masudapecten* and *Nipponopecten* , the geochronological distribution of the latter being limited only to the Early Miocene. Unlike the most thermophilic genus of the Fortipectininae, *Kotorapecten* , confined mainly to Western and Southern Japan, as well as *Masudapecten* and *Nipponopecten* , distributed only in the northern half of Honshu (*Masudapecten* noted only here) and Hokkaido, the species of the genus *Mizuhopecten* were common to both the Sea of Japan and the Pacific coasts of Japan.

In the Middle Miocene, *Mezuhopecten* found its way to Hokkaido, Sakhalin and W Kamchatka. At the same time, the range of the genus in the south decreased somewhat, being confined only to the northeastern half of Honshu; the species diversity of this genus peaked in the Middle Miocene. At the same time, the *Fortipecten* separated from them; the ancestral form for *Fortipecten* was apparently *M. matumoriensis* (Nakamura, 1940) or their common ancestor (see Kotaka, Noda, 1967).

In the Late Miocene, despite a certain decrease in species diversity, the range of the genus attained its maximum due to prochoresis into the eastern half of the North Pacific. This is documented quite well by the fossil remains of *M. mollerensis* (MacNeil, 1967). At the same time, representatives of the genus *Yabepecten* apparently found their way to the Pacific coast of North America as well.

The present-day *M. yessoensis* begins its history from the beginning of the Pliocene. Its direct ancestor is most likely *M. nakatombetsuensis* (Akiyama, 1962), known from the Upper Miocene formation of Nakatombetsu, NE Hokkaido. In the Pliocene, the range of the Yezo scallop reached Western Kamchatka (its fossil remains are found here in the deposits of the Enemten Formation), as well as Honshu. In E Honshu in the area of Kanto, the *M. yessoensis* formation in the Early Pliocene was partially replaced by the subspecies *M. yessoensis pseudoyessoensis* (Akiyama et Miyajima, 1960). Another similar species was *M. yokoyamae* (Masuda, 1962). In the Late Pliocene, due to gradual cooling (see Kafanov, 1982), the range of the Yezo scallop sharply decreased, approximating its present one.

In the Early Pliocene, the formerly unified range of *Mizuhopecten* in the North Pacific apparently underwent disjunction. In the vicinity of Washington and the adjacent areas of British Columbia and Oregon, only *M. warreni* survived. In the Late Pliocene, the species diversity of *Mizuhopecten* sharply decreased, their range approximating that of the present-day *M. yessoensis.* At the end of the Pliocene and in the Early Pleistocene, apart from the Yezo scallop, only *M. tokyoensis* (Tokungaga, 1906) had survived of the subfamily Fortipectininae; it was represented by *M. tokyoensis hokurikuensis* (Akiyama, 1962) and *M. tokyoensis sematensis* (Akiyama, 1962) from the Lower Pliocene of S Kyushu and SE Honshu, and *M. tokyoensis tokyoensis* (Tokunaga, 1906) from the Upper Pliocene and Lower Pleistocene of S Kyushu, E Honshu and Hokkaido. Only *M. yessoensis* descended from the Early Pliocene to the present.

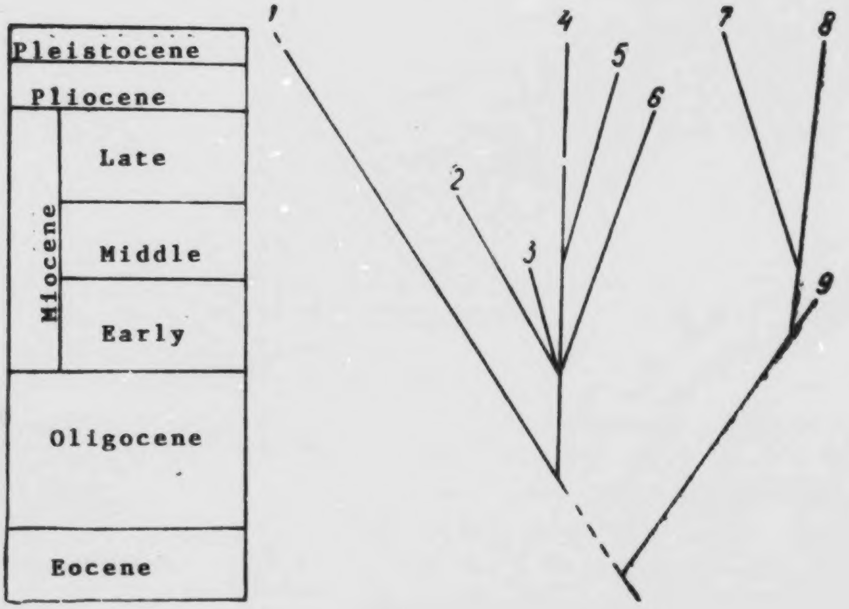

Fig. 2. Diagram of phylogenetic relations of Fortipectininae (2-6) and Patinopectininae (7-9). 1 - *Chlamys*, 2 - *Kotorapecten* , 3 - *Nipponopecten* , 4 - *Mizuhopecten* , 5 - *Fortipecten* , 6 - *Masudapecten* , 7 - *Patinopecten* s.s. 8 - *Patinopecten (Lituyapecten),* 9 - *Vertipecten*

Thus, analysis of the morphological characters of similarity and difference, as well as the phylogenetic and geochronologic relations of the subfamilies Fortipectininae and Patinopectininae (Fig. 2) brings us to the following conclusions. The Fortipectininae is a typical group of Asian Pacific origin which separated as the genus *Mizuhopecten* at the end of the Oligocene in the N Japan—Sakhalin Paleogene Province. Certain branches of the Fortipectininae (species of the genera *Mizuhopecten* and *Fortipecten*) migrated to the American coast of the North Pacific in the Late Miocene and Early Pliocene. The Patinopectininae is a group of Neogene origin; its formation and further development is associated entirely with the Pacific coast of North America. The Patinopectininae did not penetrate the NW Pacific. This is additional and very important proof that *Mizuhopecten* (Fortipectininae) and *Patinopecten* (Patinopectininae) should be regarded as two independent genera with an independent phylogeny.

2. DISTRIBUTION AND HABITAT

2.1. Boundaries of range

The Yezo scallop, an Asian Pacific Low Boreal species, lives off the northern shores of Korea, off the coast of Primor'ye (Maritime Territory) north of Chikhachev Bay, off Sakhalin Is. (western shores of the Aniva Gulf, eastern shores south of Terpeniye Gulf, off Moneron Is.), in the Southern Kurile shoals, and off the eastern coast of Iturup Is., as well as off Hokkaido and the northern coast of Honshu (Skarlato, 1981; V.I. Fadeyeva, personal communication) (Fig. 3).

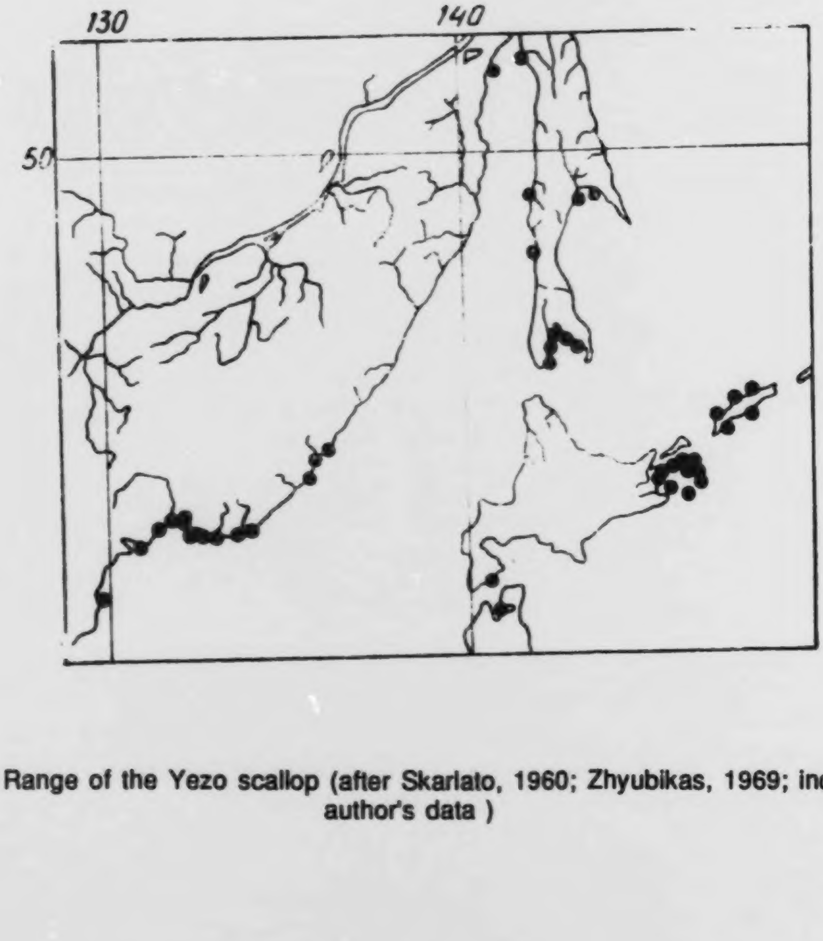

Fig. 3. Range of the Yezo scallop (after Skarlato, 1960; Zhyubikas, 1969; including author's data)

In the coastal waters of Primor'ye, the highest numbers of the scallop are noted in Posyet Bay and Peter the Great Gulf, where the species is distributed unevenly. The highest population density of the Yezo scallop is noted in the bays and gulfs, and a much smaller density off the open shores and islands. According to Biryulina (1972a), the habitats of the Yezo scallop in 1931, 1959 and 1972 remained constant, but the abundance of its concentrations diminished considerably.

Off the shores of Sakhalin Is., the Yezo scallop is found mainly in the Aniva Gulf, i.e. south of the Atlasovo settlement, on the route from the Krestyanovka settlement to the Taranai settlement, near the Prigorodnoye settlement in Bukhta Lososei [literally Salmon Bay], and from the town of Korsakov to the Busse Lagoon. The density of the concentrations and the areas populated by the species differ considerably from one area to another (Skalkin, 1966). Intensive fishing in the 1960s greatly undermined the stock of the Yezo scallop in the coastal waters of Sakhalin Is. as well (Zhyubikas, 1969).

In the Southern Kurile shoals, the Yezo scallop is widespread, but large concentrations are found only off the southeastern coast of Kunashir Is., between the islands of Tanfilyev, Yuri and Zeleny, and in the vicinity of the same islands from the side of the Southern Kurile Strait (Skalkin, 1966).

The distribution of the scallop is determined mainly by the relief and the type of bottom, the dynamic nature of the waters, and by the presence of a substrate for the settling of its larvae.

2.2. Depth

According to Razin (1934) and Skarlato (1960), the Yezo scallop is encountered at depths of 0.5-80 m, but the largest concentrations form at depths of 6-30 m. At the same time, we note a distinct correlation between the vertical distribution of substrates conducive to its existence and the abundance of its population. In the coastal waters of Primorye, in the sheltered bays and at the head of the deeply indented Posyet, Amur, Ussuri, Vostok and Nakhodka bays, slurries and clayey muds comprise the main type of bottom, while substrates suitable for the scallop (silted sand, sand, pebbles) are found only in the coastal zone. Because of this, the scallop in these areas is encountered at depths of 0.5-32 m, and it forms the largest concentrations at 6-18 m (Razin, 1934). For example, in Posyet's Expedition Bay, the scallop forms its population at a depth of 5.5-8 m (Mikulich, Biryulina, 1970). In the more open parts of Peter the Great Gulf and from Cape Povorotnyi to Vladimir Bay, it is found at depths of 10-48 m, forming mass concentrations mainly at 18-30 m.

Skalkin (1966) noted the same tendencies in the vertical distribution of the Yezo scallop for the Sakhalin-Kurile area. In Terpeniye and Aleksandrovsk bays, substrates unfavorable to the mollusks begin from 20 m. Therefore, the maximum depths at which the scallop is encountered in these areas are 23 and 21 m respectively, and its commercial concentrations are found at 7-19 m in the first area, and at 14-19 m in the second one. In the Southern Kurile area, a favourable pebble bottom occupies the coastal area up to a depth of 100 m; here the scallop is encountered up to a depth of 76 m, forming mass concentrations at 8-25 m. According to Yamamoto (1964), the scallop in Mutsu Bay of Honshu lives in the coastal areas at depths of 6-30 m, and is not encountered in the deeper parts of the bay where the bottom is covered with mud or sand. Therefore, the optimal depths (6-30 m) for the scallop are basically the same in different parts of its range.

The upper boundary at which the Yezo scallop is encountered shifts towards greater depths in the areas with strong surfs. In the open coastal waters off Sakhalin Is. and the Southern Kuriles, the scallop is often encountered only at depths greater than 10 m, sometimes 15 m, for its distribution in these areas is greatly affected by storm activity (Zhyubikas, 1969). In the sheltered bays of Primorye, where surf action is insignificant, the scallop is encountered from 0.5 m. In such areas off Sakhalin Is., e.g. in Busse Lagoon of the Aniva Gulf, the scallop lives at a depth of 2-6 m (Kulikova, Tabunkov, 1974).

The vertical distribution of the Yezo scallop is often determined by the topography of the bottom. When underwater terraces are present, which is often the case in open areas with strong currents, the Yezo scallop forms concentrations on these terraces. This creates the impression that there are several stages of optimal depths for the scallop. For example, in the coastal waters of Primorye, terraces are typically found at depths of 8-15 (mostly 10-12), 15-20, 20-26 and 35-35.5 m, which coincides with the depths of mass concentration of the scallop (8-10, 16, 20-24 and 36 m) (Razin, 1934).

The depth of distribution of various age groups also differs. Immature scallops with a shell height of less than 9 cm are the most extensively and uniformly distributed. In the coastal waters of Primorye, they are encountered at a depth of 0.5-48 m (Razin, 1934); in bays and the sheltered parts of gulfs, smaller scallops are found not only in the areas inhabited by large individuals, but also closer to shore where the larvae can find more substrate for settling. In Posyet Bay, for example, underyearlings are noted at 1.5-4.0 m, while mature individuals are found at depths greater than 3 m (Golikov, Skarlato, 1967). In the open coastal waters of Primorye, immature scallops are basically encountered only at depths greater than 16 m, due to strong surfs. In Razin's opinion (1934), the scallop, as it grows and matures, migrates to the optimal depths from the places to which it was carried during larval development. For example, in the coastal waters of Primorye, scallops with a shell 10-11 cm high are usually encountered at a depth of 0.5-46 m, individuals with 12-14 cm shells have even narrower vertical boundaries (4-40 m), and the largest individuals are encountered at 10-26 m (Razin, 1934). In the author's opinion, the narrowing of the boundaries of distribution and an increase in the density of mature scallop concentrations are necessary for successful reproduction of the scallop.

In different parts of the Aniva Gulf of Sakhalin Is., which is close to the northern boundary of the range of the Yezo scallop, the number of small individuals (12-14 cm) decreases, while the number of larger scallops (17-19 cm) increases with an increase in depth from 1 to 25 m.

2.3. Substrate

The Yezo scallop is most commonly encountered on muddy-sandy and sandy bottoms, even if the latter are in the form of islets amidst rocks; it is also encountered on a muddy bottom with a mixture of pebbles, gravel or crushed shell, which promote the growth of algae, a substrate for the young. It also lives on purely pebble, gravel and sandy bottoms (Razin, 1934). The scallop is rarely found on a purely mud bottom and rocks., the sole exception being the abundant population from Lake Vtoroye in Nakhodka Bay of the Sea of Japan, which lives on a muddy bottom. The scallop avoids large rocks, loose sand, slurry and clayey mud. According to Skalkin (1966), the boundary of distribution of the scallop by location coincides with the boundaries of distribution of the substrates preferred by it.

On a hard bottom, the scallop is usually found on its surface; where there is a strong current, it keeps its rounded margin turned toward the current, and is quite often encountered with its lower convex valve turned upward. On a soft bottom, the scallop usually buries itself in the bottom substrate slightly or up to the level of the upper valve (Razin, 1934; Skalkin, 1966). In Lake Vtoroye, the mollusks are embedded in the mud at an angle to the surface of the bottom.

Having studied the fouling and size of scallops from different populations, Razin (1934) came to the conclusion that the mollusks do not migrate from hard substrates to soft ones, and their horizontal migrations are restricted primarily by the type of bottom.

2.4. Temperature

The water temperature range in which we encounter the Yezo scallop is -2 to 26°C. The range and seasonal dynamics of temperature variation in different habitats depend on latitude, depth, exchange of water, currents, surf action and other hydrologic factors, many of which undergo change from year to year. Nevertheless, the scallop is encountered more frequently and in greater number in the areas where the water temperature in winter does not drop below -1.5°, and the temperature in summer does not rise above 18-20°C.

In the innermost parts at the northern boundary of the range, the temperature at a depth of 2-4 m (e.g. in the Busse Lagoon of the Aniva Gulf) drops to -1°C in winter, and rises to 16-17°C in August. In the other scallop habitats in this gulf, the temperature does not rise above 10.1°C at a depth of 15 m, 7°C at 20 m, and 2-3°C at 25-30 m (Zhyubikas, 1969). In the places of mass concentrations of the scallop in the Sakhalin-Kurile area, the summer temperature is mostly 6—10 or 14—15°C (Skalkin, 1966).

In the southern part of the range of the Yezo scallop (Mutsu Bay, Honshu), the temperature in winter does not drop below 4—6°C, and in summer it rises to 24°C, in some places even to 26°C for a short time.

Off the coast of Primorye, north of Cape Povorotnyi, there are areas that are affected by the cold Primorye (Maritime) current. Here, in the innermost parts of the gulfs and bays, the temperature of the surface layer of water is not higher than 18°C in summer (e.g. in the Vladimir and Olga gulfs), and drops to -1.5°C in winter. In Peter the Great Gulf, the water temperature in the shallow and sheltered bays of the Posyet and Amur gulfs is below 0°C in December-March, and drops to -1.5—1.7°C in January—February. The water here warms up quickly in spring and summer, reaching 24°C in August—beginning of September, and in some places 25—26°C for several days. In the more open parts of the range in Peter the Great

Gulf, the winter temperature up to a depth of 10—15 m is approximately the same (up to -1.5°C); the summer temperature, on the other hand, is usually not higher than 22°C, and from a depth of 15 m is lower than 20°C. In these areas, the spring—summer increase in temperature from the end of March—April (from 0°C) to the middle or end of August is usually gradual. The autumn decrease due to intensive mixing of the water masses over a short period of time, mostly from the middle of October to the end of November—middle of December, drops to 0°C.

2.5. Salinity

Unlike certain other bivalve mollusks, the Yezo scallop cannot endure drastic freshening of the water even for several days, and so it does not settle near the mouths of rivers. In winter, the salinity is close to 34‰ in practically all the places inhabited by the scallop. In summer, its value varies with the amount of precipitation and other factors. Significant freshening of the upper layers of the coastal water of Primorye is usually observed from June to September. Steady salinity conditions are basically noted in the open areas. A salinity of less than 33‰ is already rare at a depth of about 10 m. In the coastal waters of Primorye, such areas are found near the outlet capes of Peter the Great Gulf and north of Cape Povorotnyi (Razin, 1934). In the partly sheltered bays of Peter the Great Gulf, a salinity of not less than 33‰ is usually noted from a depth of 15—20 m, a 32‰ salinity from about 10 m, and a salinity of more than 31‰ throughout the year from a depth of 5 m (Biryulin et al., 1970; Stepanov, 1976). The salinity of the surface layers of water in these areas in summer is 29—32‰. The waters in the shallow, partly sheltered bays, e.g. Ekspeditsiya Bay of Posyet Bay, are the most susceptible to salinity and temperature fluctuations. However, a concentration of the Yezo scallop which lives at a salinity of 29—31‰ in summer is also found here at a depth of 5—8 m (Mikulich, Biryulina, 1970).

In the areas inhabited by the Yezo scallop in Mutsu Bay of Honshu, the salinity in summer is often lower than 32‰. In the Sakhalin—Kurile region, the majority of the open areas have stable salinity conditions. Therefore, the highest numbers of the Yezo scallop are noted in the areas with a 32—34‰ salinity.

2.6. Oxygen content

As we know, the Yezo scallop, especially its young, is sensitive to a shortage of oxygen (Handbook..., 1966). It prefers well-aerated areas with constant and fairly strong currents and periodic tides. Bregman and coauthors (1977) have established that 6 ml/l is the lower limit of the optimal content of dissolved oxygen in water.

In the open parts of the Primorye coast, the oxygen content of the water during the warm seasons is essentially 6—7 ml/l everywhere. In the partly sheltered and sheltered bays in June—October, it can be slightly lower, but it does not fall below 5 ml/l. During the cold months of the year (December—April), the oxygen content of the water in this area is the highest (up to 8—9 ml/l).

2.7. Biotic groupings

The species composition of organisms in the areas inhabited by the scallop differs with the types of bottom (Razin, 1934) and with depth (Zhyubikas, 1969), even in the same part of the range.

For example, on a pebbly—sandy bottom in the coastal waters of Primorye, the scallop is found alongside other mollusks, most commonly *Callista brevisiphonata, Mercenaria stimpsoni, Clinocardium californiense, Spisula voja, Serripes groenlandicus, Felaniella usta* and *Peronidia venulosa* . Other invertebrates frequently noted in the area inhabited by the Yezo scallop include *Patiria pectenifera, Asterias amurensis, Evasterias echinosoma, Echinarachnius parma, Strongylocentrotus intermedius* and Paguridae (Fig. 4), and the algae encountered include *Lithothamnium sp., Corallina pilulifera, Ptilota filicina, P. phacelacorpoides, Palmaria stenogona, Polysiphonia japonica, Ulva fenestrata, Agarum cribrosum, Costaria costata* and Rhodophyceae. On muddy sands and muds, the mollusks most commonly encountered with the Yezo scallop are *Crenomytilus grayanus, Scapharca broughtoni, Callithaca adamsi, Macoma calcarea, Yoldia seminuda, Modiolus difficilis, Clinocardium californiense* and *Serripes groenlandicus* ; *S. intermedius, Ophiura sarsi, Echinocardium cordatum, Stichopus japonicus, Cucumaria japonica* , Paguridae, Ascidiacea, etc. are among the other invertebrates encountered. The most common algae are *Laminaria bullata, Desmarestia viridis, Codium fragile, Ulva sp., Sargassum sp.* and certain Rhodophyceae (Fig. 5, 6) (Razin, 1934).

In the vicinity of Sakhalin Is., bivalves of the species *Swiftopecten swiftii* and echinoderms *Cucumaria japonica* and *A. amurensis* are encountered in the area inhabited by the Yezo scallop

(Zhyubikas, 1969). The Yezo scallop is often found alongside *Evasterias echinosoma* in the Aniva Gulf, and *Distolasterias nipon* in the Southern Kurile shoals.

3. MORPHOLOGY

3.1. Shell

The body of the Yezo scallop is enclosed in a calcareous shell (Fig. 7) which performs a protective function, is the external skeleton, and also assists in the movement of the animal. The shell consists of a right valve and a left one.

The shell is spheroidal. Due to the mode of life of the scallop, the bilateral symmetry of the shell has undergone distortion for the second time. The left (upper) valve is flattened, and the right valve on which the mollusk lies is convex and slightly larger, so that when the shell is closed, its edges protrude from under the upper valve. Shells of this type are called inequivalve or pleurothetic shells. The lower valve is white or yellowish-gray. The upper one has a darker colour (brownish-violet, lilac-brown), which makes the scallop less visible on the background of the bottom. The outer surface of the valves, especially the upper valve, often undergoes abundant fouling by various algae (Fig. 8), hydroids, polychaetes and barnacles (Fig. 9). The shell is sometimes damaged by polychaetous worms of the genus *Polydora*, which bore passages in the shell, and by sponges of the genus *Clione*, which live inside the valves where they form cavities and passages.

The ventral, dorsal, anterior and posterior margins of the valves are distinguished according to the position of the animal's body. The oldest part, from which shell growth begins, is called the umbo. It occupies a central position on the shell of a scallop. As to the position of the umbo, the shell of the Yezo scallop belongs to the equilateral type. Triangular lamellar processes called auricles are found on both sides of the umbo (Fig. 7). The posterior auricular processes are similar on both valves; the anterior ones have a slightly different form. In the mollusks of the family Pectinidae, the byssus emerges through a slit under the anterior auricles, and so the right anterior auricle has a so-called byssal notch (Fig. 7). The trace left on the scallop shell from the subsequent overgrowth of old parts of the byssal notch is called a fasciole. The auricles form a straight margin which is called the hinge line or the dorsal margin of the shell. The rounded margins opposite this one are called the ventral margins of the valves.

The valves are connected with each other along the straight dorsal margin by an elastic ligament composed of an organic substance known as conchin (conchiolin). The ligament of the scallop consists of two parts, an external part and an internal one (Fig. 10). The external part has the form of a very thin plate which connects the upper straight margins of the valves and attaches to special processes (nymphae) of the dorsal margin of the valves. The internal part (resilium) is far more developed. It has a triangular section, is submerged between the valves, and is located in the recess of the dorsal margin, the resilifer. True hinge teeth are lacking. The hinge is isodontal (Skarlato, 1981).

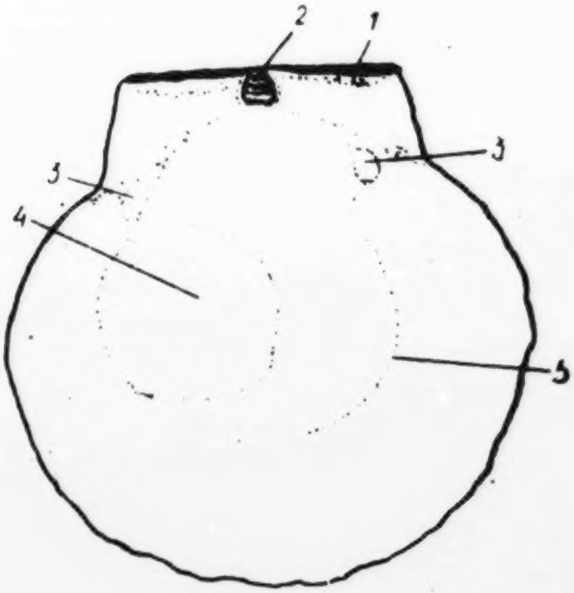

Fig. 10. Shell structure of the Yezo scallop. Interior of left valve: 1 - external part of ligament, 2 - internal part of ligament (resilium), 3 - scars of anterior and posterior ends of the velar muscle, 4 - scar of the hinge muscle, 5 - mantle line

The outer surface of the valves is covered with more or less distinct growth lines that appear as a result of the irregular growth of the mollusk (see also sect.12. Growth). This is due to both the physiological characteristics of the animals themselves, and the effect of various environmental factors on them. The surface of the valves has a radial sculpture consisting of ribs or ridges alternating with grooves. The ends of the ribs protruding along the margin of one valve fit into the corresponding intercostal depressions of the margin of the opposite valve, which promotes tighter closing of the valves and as though compensates for the absence of hinge teeth in the shell of this species.

The scars of attachment of certain muscles are distinguished on the inner surface of the valves (Fig. 10). The scar of the large adductor is located almost in the centre, and small scars of the velar muscles are found above it, anteriad and posteriad (Fig. 10). The scars of attachment of the mantle muscles, the mantle line, can be traced parallel to the lower margin at a considerable distance from it (Fig. 10).

The shell of the scallop consists of a thin organic (conchiolin) layer (periostracum), and a calcareous layer (ostracum). All the parts of the shell are secreted by the epithelial cells of the mantle from the extrapallial fluid found in the cavity between the mantle and the shell, the extrapallial cavity.

The periostracum is formed by the internal margin of the outer mantle fold, and serves as a substrate for further deposition of the organic matrix and calcium carbonate, as well as protection for the calcareous layer under it. In the mollusks of the family Pectinidae, due to the presence of one adductor (monomyarian type of structure), the pallial attachment is secondary, and the mantle—periostracum contact is very thin (Taylor et al., 1969).

The calcareous part of the shell (ostracum) consists of two layers, an outer and an inner one (Fig. 11), which are composed of one of the polymorphous varieties of calcium carbonate (calcite), and are characterized by a lamelliform type of structure (Zolotarev, 1976; Kobayashi, 1980). The smallest elements of this structure are the elongated calcite crystals which, interconnecting by their lateral faces, form striae slightly inclined to the inner surface of the shell. The aggregates of striae are grouped in lenticular scales gathered in larger structural units. The outer layer of the shell is composed of thin lamelliform scales arranged parallelly to the surface. The inner mosaic-scaly layer is characterized by large blocks of scales which are poorly oriented with the direction of shell growth (Zolotarev, 1976). At the points of attachment of the muscles to the shell, layers of a second polymorphous variety of calcium carbonate (aragonite) form (Fig. 11). These layers have a myostracum fabric with the characteristic prismatic structure. In cross-section, the prisms of the myostracum have irregular contours, and are surrounded by a thin layer of organic matter.

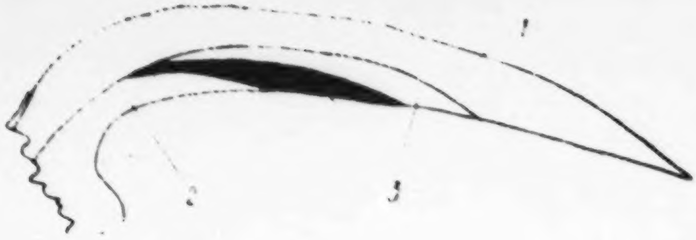

Fig. 11. Diagram of internal structure of scallop shell: 1 - outer layer, 2 - inner layer, 3 - myostracum

The shell of the scallop has a different structure at the early stages of biological development. The veliger has the D-shape typical of bivalve larvae. The shell at this stage (prodissoconch I) is secreted by the shell gland, and is composed of an organic substance called conchiolin. At the veliconch stage (prodissoconch II), the shell is formed by the epithelial cells of the mantle margin, and is composed of aragonite (Iwata, Akamatsu, 1975). It consists of fine granular crystallites which form the granular prodissoconchal fabric. The shell of a veliconch is triangular—ovate. The left valve is slightly wider than the right one (Maru, 1972). The umbones are small, spheroid, and protrude slightly above the hinge line. The taxodont hinge consists of rectangular teeth arranged along the edges of the provinculum. A fully formed larva has 5 teeth on each side of the hinge line, and a medial ligament. A concentric and radial sculpture is clearly visible on the thin shell. Prior to settling, the veliconchs attain a length of 260—285 µm and a height of 240—350 µm (Kulikova et al., 1981). The shell of spat (dissoconch) begins to acquire the form of adult mollusks.

The maximum size (height of the shell) of mature individuals of the Yezo scallop is 220 mm (Skalkin, 1966; Mandryka, 1979).

3.2. Internal organs

Since the time Ivanov and Strelkov put out their anatomical atlas (1949) with diagrams of the principal organs of the scallop, there has been no scientific paper devoted to the morphology of the internal organs of this species. The descriptions given here are based on original material collected by the author of the section in Ussuri Bay of the Sea of Japan in the spring of 1982. Ivanov and Strelkov's data have been detailed by us considerably, and the names not encountered in the anatomical atlas have been borrowed from other authors (Atkins, 1937; Graham, 1937, 1949; Yonge, 1949, 1957; Owen, 1955, 1966; Purchon, 1956, 1957, 1958, 1960; Gilmour, 1964; Hoyle, 1964; Reid, 1965; Ghiretti, 1966; Hill, Welsh, 1966; Bernard, 1971; Waller, 1980; Skarlato, Starobogatov, 1972).

The body of the scallop, which is enclosed in a bivalve shell, consists of a mantle which lines the shell, a large adductor, a pedal-visceral mass, ctenidia, a labial apparatus, a digestive gland, a pericardium (cardiac sac), gonads and nephridia.

The mantle (figs. 12, 13) is formed by the left (upper) and the right (lower) lobes which coalesce in the dorsal part. In turn, the lobes subdivide into two parts, a thin-walled part which lies adjacent to the adductor in front and covers the liver from the sides, and a thickened part which lines the peripheral zone inside the valves.

The thin-layer mantle (tm) is translucent, and is pierced near the adductor by well-defined dichotomizing nerve fibres (nf) that radiate from the branchial arch. From the side of the mantle cavity, the thin-layer mantle is covered with ciliated epithelium, the cilia of which form grove-like polygonal accumulations with diffused boundaries. The parts of the thin-layer mantle enveloping the liver laterally are also translucent; at the points of attachment of the oral lobes and in the intervals between the adductor and the liver, they are pierced by bundles of thin collagen-like fibres. The structure of the thin-layer mantle of the left and right lobes is similar, i.e. a layer of dense connective tissue with blood vessels and nerve fibres is enclosed between the epithelium of the outer and inner surfaces.

A thickened mantle (sm) forms the marginal zone which appears as a wide band distad to the pallial line (pl). The band narrows significantly dorsally. As to its structure, the thickened mantle can be divided into the mantle proper, a fold or velum (ifm), and a papillate crest (mfm).

The outer surface of the mantle proper (Fig. 13, B) is covered with an epithelium with a poorly discernible reticulate structure. Punctate accumulations (microtubercular processes) are visible within the polygonal cells. Under the epithelium, we find a layer of radial muscle fibres (rmf) gathered in wide, distally diverging bundles with connective tissue between them. The proximal ends of the bundles form a slightly raised concentric ridge which adheres to the shell and leaves an impression (pallial line) on it. A thick layer of concentric muscle fibres (cmf) lies under the epithelium on the inside of the mantle (Fig. 13, C). In the middle of the mantle, the surface of the layer is rugose; the grooves between the rugae are deep and slightly undulate. The proximal part of the mantle is usually smooth, with a weak radial striation. Small concentric rugae separated by narrow grooves are found on the apical parts on the inside of the mantle. The inner space between the layers of radial and concentric fibres is filled with connective tissue.

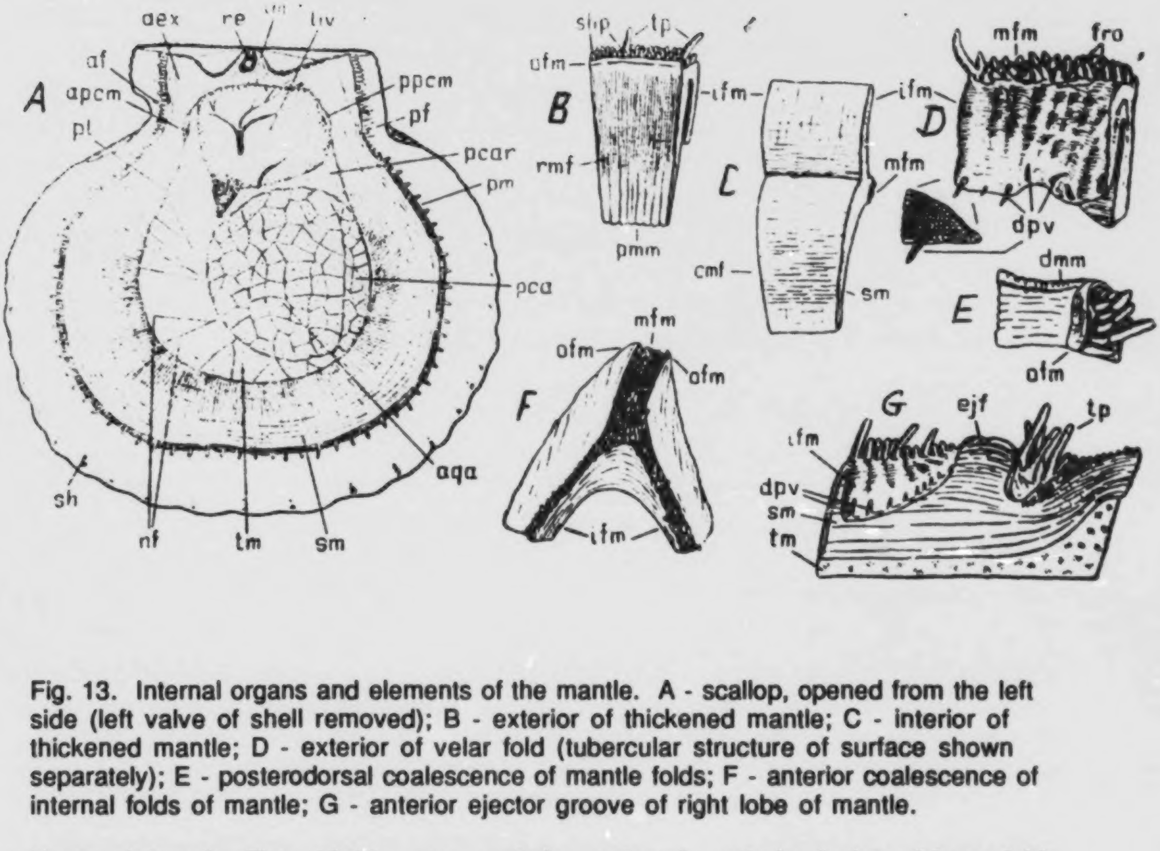
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Fig. 13. Internal organs and elements of the mantle. A - scallop, opened from the left side (left valve of shell removed); B - exterior of thickened mantle; C - interior of thickened mantle; D - exterior of velar fold (tubercular structure of surface shown separately); E - posterodorsal coalescence of mantle folds; F - anterior coalescence of internal folds of mantle; G - anterior ejector groove of right lobe of mantle.

Nomenclature for Figs. 13-16: aao - anterior aorta; af - anterior fusion of inner fold of mantle; ag - anterior part of intestine and sac of crystalline style; ao - aorta; apcm - anterior attachment of pallial concentric muscle to shell; aqa - anterior part of adductor; asa - anterior sorting area of stomach; bao - bend expansion of aorta; bc - byssal cleft; bcct - blood vessel of gill arch; bcr - base of branchial crest; bdg - base of dorsal groove; bg - byssal gland; bgsh - base of gastral shield; caao - continuation of anterior aorta; car - cardinal ventricle; cmf - concentric muscle fibres of mantle; cr - branchial crests; ct - ctenidia; dc - digestive cecum; dcr - dividing crest of hooded expansion and left cecal pocket; dex - dorsal expansion of mantle; dd - digestive diverticulum; ddlp - digestive diverticulum of cecal pocket; dg - dorsal groove; dglp - collecting groove of right oral lobes; dlse - descending limb of left external demibranch; dmm - dorsal margin of mantle (pallial crest); dpv - distal papillae of velar fold; dwp - dorsal wall of pericardium; eaao - exit of anterior aorta; eag - exit of anterior part of gut and sac of crystalline style; ehsh - erosion head of gastral shield; ejf - ejector fold of mantle (groove); emg - exit of midgut; eo - oesophagus; eoc - ridge of oesophageal exit; eoo - opening of oesophagus; etsh - erosion teeth of gastral shield; frp - photoreceptor organ; fs - fissure of gill connection; ger - hollow s-shaped connections of branchial crest; ggh - collecting groove of hooded expansion; glp - digestive grooves of left cecal pockets; gsh - gastral shield; h - hooded expansion; htsh - trough process of gastral shield; iag - inlet at starting point of gut; ifm - internal (velar) fold of mantle; ilp - interior of oral lobe; im - isthmus of mantle; img - inlet of midgut; isah - incurrent sorting area of hooded expansion; la - labial apparatus; lavo - left atrioventricular opening; lcex - left expansion of cardial ventricle; liv - digestive gland; ll - lower lip; llll - lateral lobules of lower lip; lllp - left lower oral lobe; llul - lateral lobules of upper lip; lp - left cecal pocket; lsg - longitudinal sorting grooves of oral lobe; lulp - left upper oral lobe; m - mouth; mbls - gill arch of left inner demibranch; mdg - main digestive groove; men- meniscus of gastal shield; mfm - medial fold of mantle (papillate margin); mg - marginal groove or oral lobe; migp - main incurrent groove of left cecal pocket; mlg - midgut; mlll - main lobules of lower lip; mlul - main lobules of upper lip; ms - transitional membrane connective (seam) of descending and ascending limbs of demibranch; msa - main sorting area of stomach; nef- nephridia; nf - nerve fibres; ofm - outer fold of mantle; ol - oral lobes; olp - outer surface of oral lobe; p - foot; pao - posterior aorta; pca- posterior of adductor; pcar - pericardium; pdd - opening of posterior digestive diverticulum; pf - posterior fusion of internal fold of mantle; pgsh - posterior wing-like expansion of gastral shield; pl - pallial line; plcr - lamellar apex of branchial crest; plct - branchial lamellae; pm - papillate margin of mantle; pmm - proximal margin of thickened mantle; ppcm - posterior attachment of pallial concentric muscle to shell; pps - posterior end of left outer demibranch; pym - pedal-visceral mass; pwc - posterior wall of hooded expansion; pwst - posterior wall of stomach; pwvm - posterior wall of visceral mass; ravo - right atrioventricular opening; rbc - ridge of byssal cleft; rcex - right expansion of cardial ventricle; re - resilifer; rec - posterior (straight) section of gut; rgh - groove of food particle removal from hooded expansion; rglp - excretory grooves of cecal pocket; rgsh - removal groove of horseshoe-shaped sorting area; rllp - right lower oral lobe; rlsg - ridges of longitudinal sorting grooves of oral lobe; rmf - radial muscle fibres of mantle; rml - right lobe of mantle; rulp - right upper oral lobe; sac - sorting area of cecum; sah - horseshoe-shaped sorting area of stomach; sap - sorting area of left cecal pocket; sc - distal cleft of foot; seh - saddle of erosion head of gastral shield; sgh - sorting groove of hooded expansion; sh - shell; shp - short papillae of velar fold of mantle; sigp - auxiliary groove of cecal pocket; sm - thickened mantle; st - stomach; tgsh - trough of gastral shield; tm - thin-layer mantle; tmct - marginal denticles of branchial lamellae and filaments; tp - long papillae of velar fold of mantle; ul - upper lip; ulse - ascending limb of left outer demibranch; vwp - ventral wall of pericardium

The velar fold (Fig. 3, D) is the incurved apical margin of the thickened mantle. When the valves are closed, the velar fold overlies the inner surface of the mantle. Its width in the ventral part is about one-half of the width of the marginal zone of the mantle proper, and it is 3 times narrower than the mantle in the posterior and anterior parts. In the dorsal part, the velar folds of the left and right lobes form fusions (af, pf).

The inside of the fold is covered with a ciliated epithelium, under which concentric muscle fibres are visible. The fibres are gathered in thickened bundles near the base of the fold. The diameter of the bundles gradually diminishes apically, and the fold itself becomes thinner. Radial muscle fibres predominate at the apical margin. Rows of tuberculate processes on the outer surface of the velum form radial-concentric structures. In cross-section, the tubercles are isometric, with rounded apices; they are closely spaced in concentric rows separated by grooves. The rows are also dissected by radial irregular grooves separated by wide folds of radial muscle fibres overlain by a thin layer of concentrically oriented fibres. Black pigment spots are sparsely distributed on the outer surface of the velum. Thin and long papillae with acuminate apices (dpv) are found along the apical margin. The papillae are usually horn-shaped, and are located at some distance from the velar margin. Their surface is covered with tubercles. The ejectory aperture serves as the boundary of the dorsal distribution of apical papillae.

Near the point where the mantle passes into the dorsal expansion (dex), which repeats the contours of the shell auricles, the velar fold narrows to 3—5 mm, and forms the ejectory furrow (Fig. 13, G) (ejf). At this point, the narrow margin of the velar fold that frames the furrow is thickened and highly pigmented. The inside of the mantle is striated by thin concentric grooves, and the ridges separating the grooves bear rounded microprocesses on their apices. The dorsal margin of the ejectory furrow is covered with long papillae.

The papillate crest (mfm) is the distal margin of the mantle proper, which bears up to 5-6 rows of closely spaced papillae. The papillae are digitate, with acuminate ends and a rounded or oval cross-section in which the elongated axis usually runs parallel to the margin of the mantle. Short (up to 2—3 mm) and long (up to 10—12 mm) papillae are characteristic. Hemispherical photoreceptor organs (frp), mantle eyes surrounded by a dark pigment, are found between them. The short papillae are white, and the sparsely distributed long ones have a yellowish hue. The more abundant short papillae (shp) are located near the outer surface of the mantle, which lies adjacent to the shell; it is separated from it by a well-defined outer fold (ofm). The surface of the long (tp) and short (shp) papillae are covered with concentric rows of microprocesses, and these rows are separated by grooves. In addition to the transverse grooves on the flattened distal and proximal sides of a papilla, there is one longitudinal groove which extends from its base to its apex.

The papillate crest extends along the apical margin of the mantle, and continues along the anterior and posterior margins of the dorsal expansion. Here it is formed by the fused crests of the left and right pallial lobes (Fig. 13, F). The fusion of the crests is found at the base of the dorsal expansion; ventrad of the latter is the point of fusion of the reduced velar folds consisting of thickened concentric fibres. The hinge line, or pallial crest (dmm), is the dorsal boundary of the papillate crests. The epitheliomuscular thickening of the crest (Fig. 13, E), composed of concentric fibres of the mantle proper, ends in a scalloped margin capable of straightening out during ligament growth. In the medial part of the crest, there is a mantle isthmus (im) which surrounds the resilifer (re) from three sides.

The adductor (Fig. 13, A; 14, E) occupies the central part of the mollusk's body, and consists of an anterior region (aga) and a posterior region (pca), which differ in the structure of the muscle fibres. The anterior subcylindrical region is formed by cross-striated muscle fibres gathered in bundles. In cross-section, these bundles are triangular, square or polygonal, and are separated from each other by a thin layer of connective tissue. The posterior region is about 3-5 times smaller than the anterior one; its form in cross-section is similar to a segment, and consists of smooth muscle fibres. The anterior and posterior regions are separated by a layer of connective tissue. The same type of tissue covers their lateral surface, and fuses with the thin-layer mantle of the left and right lobes.

The pedal-visceral mass (Fig. 14, E, F-I) is a flattened curved part of the body, which encompasses the adductor from the front. The dorsal end of the pedal-visceral mass (pvm) adheres to the digestive gland; the acuminate posteroventral end is free. The inner concave margin is expanded; the dense connective tissue (pwvm) covering it for about 2/3 of its length adheres to the connective-tissue membrane of the adductor. The posterior end of adherence is split into two bundles that extend from the long axis of the visceral mass. The bundles consist of collagen-like fibres that become lost in the membrane of the adductor.

A small foot (p) extends from the anterior part of the dorsal end of the visceral mass. It is cylindrical, with a gently rounded apical part; the dorsal and lateral sides are rugose, and covered with a ciliated epithelium in which black pigment spots are scattered sparsely. The concentric ridges of the rugae bear rounded or oval tubercles. Circular muscle fibres are clearly visible under the epithelium. The byssal cleft (bc), surrounded by small sinuate rugae, is found on the ventral side. Near the byssal cleft under the epithelium, we find longitudinal muscle fibres, and under them a layer of circular fibres. The byssal cleft is deep, and extends almost to the central long axis of the foot. The cleft is framed by a ridge (rbc) of fused longitudinal and circular fibres, and the walls of the cleft are composed of longitudinal fibres covered with epithelium. The inner space between the wall of the cleft and the longitudinal-circular layer is filled with loose connective tissue. At the base of the foot, there is a conical byssal gland (bg), the expanded part of which occupies the middle part of the foot. The tapered end of the gland is curved slightly to the left, and goes into the visceral mass. From the outside, the gland is surrounded by a thick tissue which passes into the walls of the byssal cleft. The apical end of the foot has a short ventral cleft (sc) at the continuation of the byssal cleft. The walls of the short cleft are covered with a thick yellowish epithelium. The lateral parts of the apical end of the foot bear concentric ridges of small spherical tubercles.

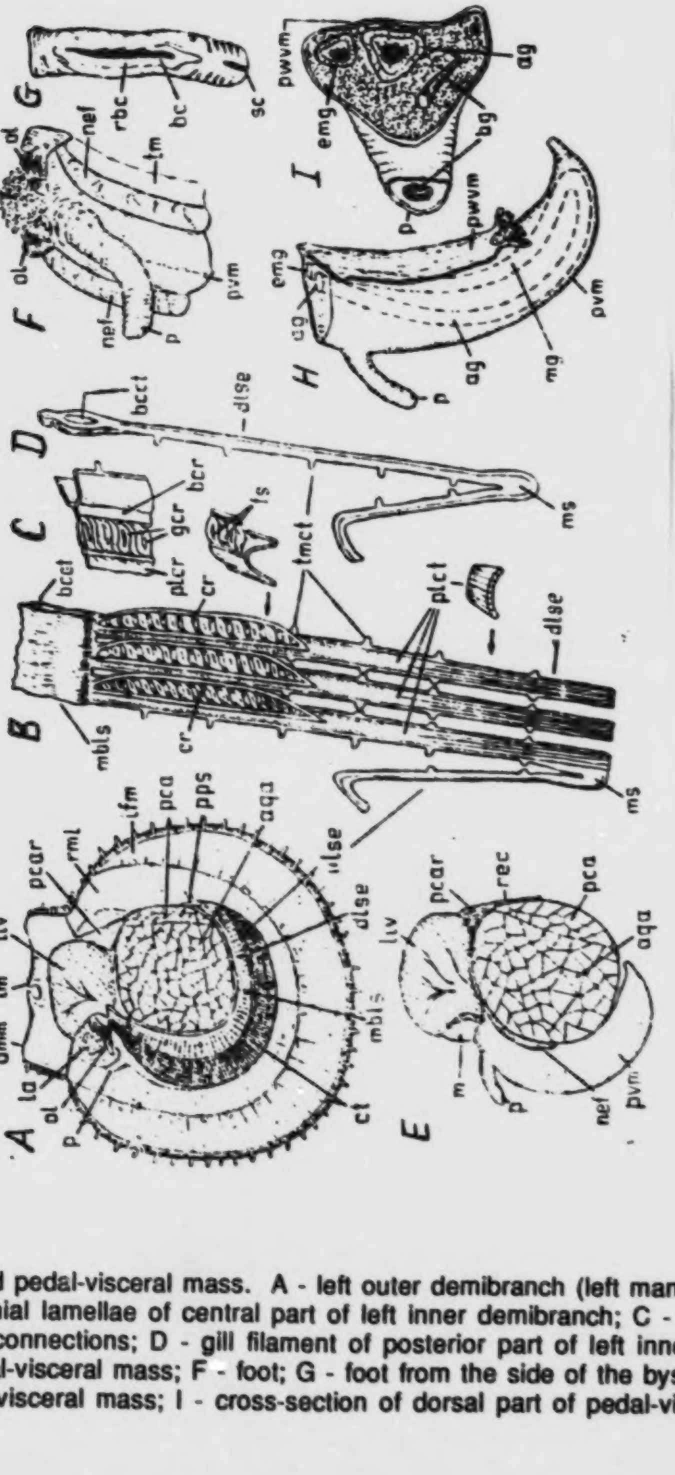
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Fig. 14. Ctenidia and pedal-visceral mass. A - left outer demibranch (left mantle lobe removed); B - branchial lamellae of central part of left inner demibranch; C - branchial crest with connections; D - gill filament of posterior part of left inner demibranch; E - pedal-visceral mass; F - foot; G - foot from the side of the byssal cleft; H - gut inside pedal-visceral mass; I - cross-section of dorsal part of pedal-visceral mass

The anterior and lateral surfaces of the visceral mass are covered with a ciliated epithelium. Under the epithelium, longitudinal and circular muscle fibres, intersecting each other at an acute angle, form a thin-layer epitheliomuscular membrane. Inside the membrane, we find the sac of the crystalline style (ag), which passes into the midgut (mlg). Emerging from the digestive gland, the anterior part of the gut and the sac, lined with a ciliated epithelium, at first pass along the posterior wall of the visceral mass, and then move closer to the centre. In the posteroventral part, which occupies about one-half of the visceral mass, the foregut and the sac narrow to the diameter of the midgut which passes along the anterior wall of the visceral mass. In the apical part, the gut forms a sharp loop. The ascending anterodorsal-median part of the gut gradually shifts from the centre of the visceral mass, first to its right wall, and then to the posterior wall, occupying a posterolateral position near the digestive gland. The point of entry of the midgut into the digestive gland (emg) is located to the right of the exit of the sac of the crystalline style. The inner part of the visceral mass is filled with fibrous loose connective tissue. Flocculent greenish aggregates are usually encountered inside the midgut. In the sac of the crystalline style in freshly caught mollusks, there is an elastic translucent rod (crystalline style) which narrows towards the apical end of the visceral mass.

The ctenidia (Fig. 14, A-D) consist of a left and a right gill, which bend round the adductor anteroventrally, and are located laterad of the pedal-visceral mass. The gills are attached to the adductor by means of a membranous base, dense and thickened connective tissue which forms the gill arch (mbls). The anterior end of the arch adheres to the connective-tissue membrane of the digestive gland. The collagen-like fibres of the posterior end of the arch (pps) are split into two branches. One branch near the anus goes into the tissue enveloping the adductor, and the second one radiates in the thin-layer mantle, reaching the pallial crest in some places.

Each gill consists of demibranchs, an outer and an inner one, and they in turn consists of an ascending limb (ulse) and a descending one (dlse). The descending limbs, fusing with the dorsal margins, connect with the membranous base. The dorsal margins of the ascending limbs are free. A demibranch is divided into thin narrow lamellae (plct) which fuse along the dorsal margins of the descending limbs near the gill arch. The cross-section of the lamellae is variable. The lamellae are flattened laterally near the membranous base; in the middle of the descending limb, they are trough-shaped, with the convexity turned to the ascending limb; the descending limb is ventrally slightly convex and striated by 6-8 longitudinal grooves along which the lamella splits into filaments. The apical margin of the descending limb is formed by half-split lamellae-filaments which change their direction from descending to ascending. On the inside, the curvature has a small connector (ms). The ascending limb consists of filaments which are recurved at the free proximal margin in the opposite direction to the descending limb and the fused ends which are also recurved.

Along both margins of the lamella and the anteroposterior margins of the filament, we find small processes in the form of denticles (tmct) directed at the descending limb of the demibranch distally, and at the ascending limb proximally. The denticles are composed of dense, white, opaque tissue (as are the margins of the lamellae), and are found at some distance from each other, forming with the denticles of the adjacent lamellae and filaments rows parallel to the gill arch. Extending from the gill arch along the convex side of the descending lamellae to one-half or one-third of the length of the lamella is a high crest (cr) which recurves backward and overlaps the adjacent crest of the posterior lamella with its apex. The lamellar base (bcr) and apex (plcr) of the crest are formed by dense connective tissue. Transverse S-shaped connections (gcr) are found between the base and the apex of the crest. The connections are lenticular in cross-section, hollow inside, and connected with the vessel extending along the base of the lamellar apex. Near the middle of the descending limb, the apex of the crest fuses with its base, and the crest disappears. Crests are encountered in the anterior and central parts of the demibranch, which consist of lamellae. There are no crests on the tapered posterior part of the demibranch, which is formed by filaments.

The labial apparatus (Fig. 15, A-D) consists of an upper lip (ul) and a lower lip (ll), and of continuations of the lips on both sides, the upper (outer, lulp) and lower (inner, lllp) oral lobes.

The upper lip is divided into two main lobules (mlul) consisting of processes expanding apically and crowned by a fimbriate tissue of small papillae. The sides of the lobular stem are smooth; the cross-section of the lobules is spherical or oval, increasing towards the base. Secondary lobules branch out near the apical part of the main ones. Their apexes, dotted with small papillae, come into contact with their separated margins and form a single convex-tubercular apex of the main lobule. On the inside, the lobule is composed of a dense non-fibrous tissue pierced by large ducts. A layer of longitudinal muscle fibres is observed under the thin epithelium. The main lobules of the upper lip are located close to the median line of the mouth, and are separated by a space almost as wide as the thickness of the lobular stem. Two secondary lobules (llul) are usually found to the left and to the right of the main lobules. The internal structure of these lateral lobules is similar to that of the main ones, but in form and size they correspond to the secondary lobules that branch out from the main ones. Altogether, the upper lip of a mature mollusk bears 10-12 secondary lobules which form 6-8 separate processes.

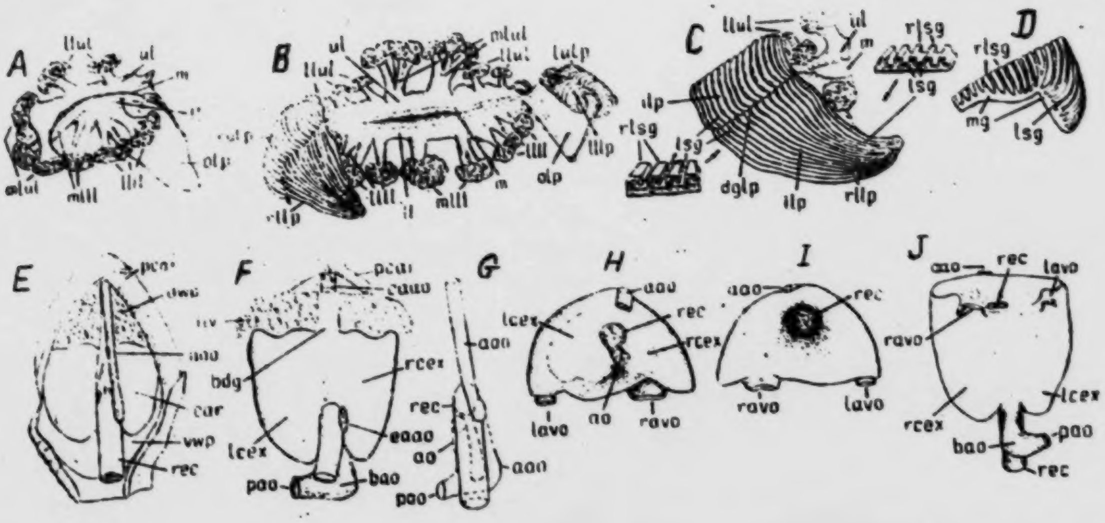
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Fig. 15. Labial apparatus and heart. A-left margin of mouth with opened lateral lobules; B-labial palps and oral lobes; C-inside of right oral lobes, proximal and distal sections of their sorting grooves; D-marginal groove of distal part of lower oral lobe; E-heart with exposed dorsal wall of pericardium; F-dorsal side of cardial ventricle without pericardium and anterior aorta; G-branching of aorta; H-posterior side of cardial ventricle without aortic expansion and posterior part of gut; I-anterior side of cardial ventricle; J-ventral side of cardial ventricle

The lower lip bears 9 separate processes, 3 of them being the main lobules (mlll) located in the median part of the mouth. They are slightly smaller than the main lobules of the upper lip. The lateral lobules (llll) are long and slender; their expanded bases are fused with each other, and the cross-section is close to lenticular in form. The internal structure is similar to that of the main lobules.

When functioning, the main lobules of the upper lip go into the wide spaces between the lobules of the lower lip, while the lobules of the lower lip go into the median space of the upper lip and in the spaces left and right of the main lobules. The way in which the lateral lobules close can vary. In some specimens, the lateral lobules of the lower lip alternate with the same lobules of the upper lip, while in other specimens the lateral lobules of the lower lip go into the secondary bifurcations at the apexes of the main lobules of the upper lip, and the lateral lobules of the upper lip are underdeveloped. When the labial palps are closed, they form a solid junction in the central part of the mouth, which closes the latter in front. The junction of the lobules varies in density and form at the margins of the mouth. Sinuate ducts remain between the walls of the lateral lobules.

Near the corners of the mouth, the upper and lower lips pass into the upper (rulp, lulp) and lower (rllp, lllp) oral lobes which are long and wide lamellar processes separated from each other by a deep transverse groove (dglp). The proximal end of this collecting groove is found at the continuation of the joining line of the mouth (m); the distal end is slightly lowered ventrally towards the anterior margin of the ctenidia. The base of the groove adheres to the inner surface of the mantle by means of dense fibrous connective tissue. The lobes are pteroid-triangular, with a gently tapering distal margin. The inner locking surfaces of the lobes bear longitudinal grooves (lsg) which fall into a transverse collecting groove at the base of the lobe. The longitudinal grooves are separated from each other by ridges (rlsg) which taper out at the distal end of the oral lobe (Fig. 15, D). The cross-section of the ridges near the distal margin is angular; in the proximal part, the rectangular ridges pass into crests with acuminate apexes. At the same time, the apexes of these crests bend at a right angle to the mouth, and the crests themselves outwardly resemble the rectangular ridges. The outer surface of the lobes (olp) is smooth; intersections of longitudinal and transverse muscle fibres are seen under the epithelium. The join surface is covered with ciliated epithelium, under which a layer of longitudinal and transverse muscle fibres is also found. The space between the outer and the inner layers of these fibres is filled with loose connective tissue with wide ducts.

The digestive gland or, as it is sometimes called, the liver of the scallop (Fig. 16) has an oval-elongated form (liv), and is pierced by digestive ducts and blood vessels. The stomach (st) is found inside the gland. The gland is located dorsad of the adductor, and is attached to its cylindrical surface by means of lamellar connective tissue which encloses the sides of the adductor and digestive gland, and also by means of fibrous connective tissue which forms lateral strands that extend from the anterior end of the gland to the visceral mass. The sides of the gland are covered by the thin mantle which passes dorsally and posteriorly into thickened tissue pierced by thin collagen-like radial fibres. The dorsal side of the gland is attached to the mantle lobes converging here by means of a connective-tissue crest consisting of an expansion of the thickened mantle. In the hollow base of the crest, there is a wide dorsal groove (dg) which begins at the posterior end of the gland, and emerges at the anterior end. The posterior end of the gland is slightly drawn out and acuminate; it ends in the opening of the posterior part of the gut (emg) found in the median plane. The ventral side of the gland is flattened; a longitudinal convexity formed by the gut (mg) is observed near its right side.

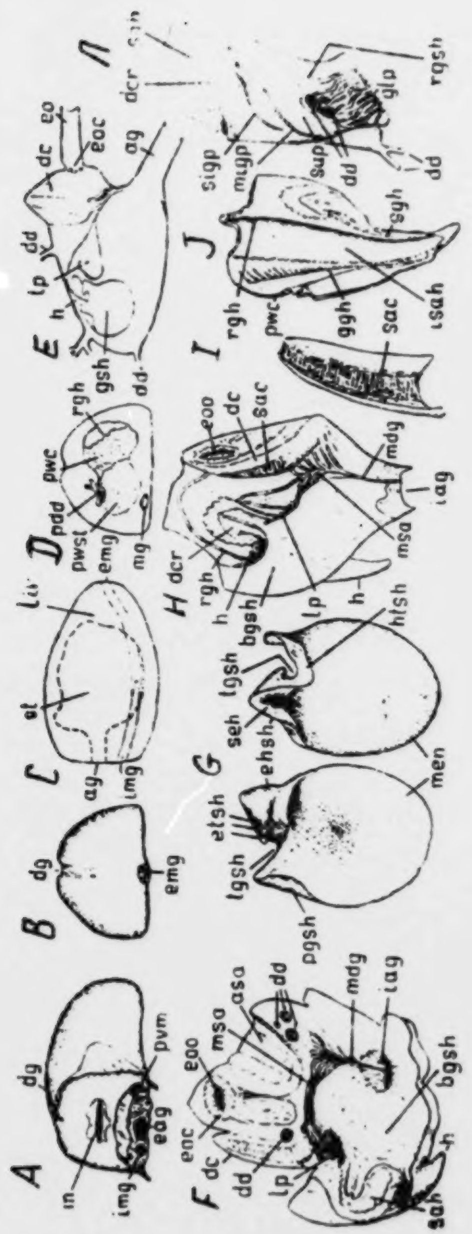
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Fig. 16. Digestive gland (liver) and stomach. A-anterior view of digestive gland (lobules and oral lobes removed); B-posterior view of digestive gland; C-ventral side of digestive gland; D-section through digestive gland and stomach near its posterior wall; E-location of main elements of stomach; F-left anterior and ventral walls of stomach; G-gastral shield from functional and opposite side; H-hooded expansion, left cecal sac and cecum; I-digestive cecum; J-hooded expansion; K-left cecal sac

At the anterior slightly convex end of the gland, there is a slit-like oral aperture which leads to a short oesophagus. The latter opens into a small sacciform stomach which, like the oesophagus, is completely surrounded by tissue of the digestive gland. The gland is connected with the stomach by several large ducts.

In the stomach, we distinguish the dorsal and ventral sides, the right and the left halves, as well as the fundus and the top. The right part of the stomach in the Yezo scallop is more developed. On the dorsal side of the stomach, we find the opening of the oesophagus and the food-receiving chambers (dorsal hood and food-sorting cecum). A sorting system with duct openings of the digestive gland is found in the fundus. On the ventral side, the stomach enters the foregut, from which the crystalline style enters the stomach.

The pericardium (Fig. 15, E-J) (pcar), which encloses a three-chamber heart consisting of two auricles and one ventricle (car), occupies a posterior position between the digestive gland and the adductor at the base of the dorsal expansion. Its anterodorsal wall (dwp), which, like the other walls, is composed of thin-fibre elastic connective tissue, envelopes the posteroventral rounded part of the digestive gland, going into the anteriorly narrowing space between the gland and the surface of the adductor. The opposite ventral wall (vwp) covers the cylindrical surface of the adductor. The posterior wall is oval, and coalesces with the connective-tissue membrane of the gland and the thickened tissue of the cylindrical surface of the adductor. The lateral rounded-triangular walls of the pericardium laterally confine the anteriorly narrowing space.

In the anterior part of the narrowing space, we find two auricles shaped like thin-walled hollow petals with dissected margins. The petals contain a dense network of interweaving blood vessels and trabeculate connections, and the walls are composed of a dense white tissue. The auricles are connected with the cardinal ventricle (car) in the posterior expanded part of the pericardial cavity by means of flattened, widely branching vessels.

The ventricle has a complex form. Its posterior wall has a longitudinal-cylindrical convexity. Extending along the axial part of the wall is a groove (bdg) which is lined with elastic connective tissue grown together with the covering tissues of the ventricle. There are two openings in the ventral part of the groove. The hindgut (rec), which is directed ventrally, emerges from the central opening, and the anterior aorta (eaao) comes out of the smaller lateral opening. The ventral wall of the ventricle bears two gently tapering processes or expansions (rcex, lcex) separated by a longitudinal groove; the left expansion is larger than the right one. The anterior wall of the ventricle is flattened, and slightly concave in the axial part. On the left and right margins of the wall near the point where it passes into the dorsal wall, we find the respective left (lavo) and right (ravo) atrioventricular openings which connect the ventricular chamber with the auricles. The openings are surrounded by a high, rather prominent ridge. The right opening is about twice as wide as the left one. The dorsal wall of the ventricle is applanate-concave, and drops infundibularly to the entry of the hindgut which is offset from the centre to the posterior wall.

The walls of the cardinal ventrical are composed of densely elastic epicardial tissue and coarse-fibre myocardial tissue. The inner surface of the walls bears numerous trabeculae of different order. The dominant role belongs to the anteroposterior trabeculae that dissect the ventricular chamber into small subchambers connected by wide passages and ducts. The longitudinal thickening of the posterior wall, which contains the rectum, divides the ventricular chamber into the left and right expansions which interconnect at the anterior wall. On the ventral wall under the septal thickening, we find the outlet of the main aorta (ap) which branches out at the swelling point (bao) into the posterior (pao) left-bound and anterior (aao) right-bound vessel which then emerges on the surface of the posterior wall of the cardinal ventricle.

4. NERVOUS SYSTEM

4.1. Anatomy and Histology

The nervous system of the Yezo scallop, like that of other bivalves, has a ganglionic structure. Having removed the right valve of the shell and turned up the oral lobes, we can easily find the pedal ganglia. The ganglia lie close to each other, and are separated by a noticeable constriction. The cerebropleural ganglia are drawn up to them. They are joined to the pedal ganglia by short connectives about 2-3 mm in length. The cerebropleural ganglia lie symmetrically opposite each other on both sides of the oesophagus, and are connected to each other by a 20-25 mm commissure which passes above them. The ganglia usually have a dull yellowish colour. The visceral ganglion of the scallop is located in the lower part of the body, on the surface of the adductor; it is covered by the gonad, and is joined to the cerebropleural ganglia by connectives. This ganglion is up to 4 mm long and 2-2.5 mm wide. In the Yezo scallop, the visceral ganglion is unpaired, apparently the result of the fusion of the visceral ganglia.

The ganglia of the scallop, as in other protostomatic animals, are constructed in the same way. Under the capsule, we find a cortical layer formed by neuron bodies; their processes, which converge in the centre of the ganglion, form the neuropile. The capsule of the ganglion, or perineurium, is formed of dense connective tissue, the same as in other mollusks; it apparently performs a protective, supportive and, because of the presence of hemolymphatic vessels, a metabolic function in the body. Collagen fibrils and anastomosing collagen plates form the base of the epineural layer.

Two types of cells, fibroblasts and macrophages, are found between the fibres and the plates. Individual muscle cells are encountered on the periphery. Embedded in the capsule are hemolymphatic vessels which merge to anastomosing open lacunae. Nerve fibres with expansions filled with agranular synaptic vesicles sometimes come into contact with the walls of the vessels. The capsule is covered with one or two rows of flattened fibroblasts joined together by dense contacts.

The epineurium and hemolymphatic lacunae are separated from the neurons by a layer of branching hyaline cells. The neuron bodies form the cortical layer of the ganglion. The largest neurons lie directly under the capsule. The peripheral nerves arise from groups of cells called gangliomers. The neuropile, formed by axions gathered in bundles and partly covered by the glia, forms the central principal mass of the ganglion.

The number of neurons in the ganglia of the animals was counted with the fragments of the neurons containing a nucleolus taken into account. The accuracy of the count suffered because of the presence of large and double nucleoli, their eccentric position, and the high degree of variability of the neurons themselves, among which small cells predominate. With these circumstances taken into account, it can be said that the content of neurons in the ganglia differs, but there are no differences between the right and the left ganglia (Table 1). The largest number of neurons is observed in the visceral ganglion, and the total number of nerve cells in the ganglia of the scallop is 236,287±5522.

Table 1. Number of nerve cells in the ganglia of the Yezo scallop

Ganglia	No. of neurons counted	20% correction	
		for eccentric position of nucleolus	for two nucleoli
Cerebropleural			
right	40,486±912	36,438±821	32,390±730
left	47,700±377	42,930±340	38,160±303
Visceral	64,649±2081	58,186±1873	51,721±1665
Pedal			
right	40,626±683	36,564±615	32,502±547
left	42,826±1449	38,554±1305	34,262±1161

Table 2. Volume of neurons, their nuclei and nucleoli (μm^3)

Neurons	Visceral	Cerebropleural	Pedal
Large			
body	6272±207	2891±132	4018±184
nucleus	225±11	131±7	148±8
nucleolus	22±1	12±1	13±0.5
Medium			
body	2406±108	2105±127	2327±113
nucleus	258±11	145±5	99±5
nucleolus	17±1	8.6±0.3	8.0±0.5
Small			
body	395±17	611±29	679±24
nucleus	81±5	79±4	76±21
nucleolus	4.8±0.3	5.6±0.5	4.6±0.2

Table 3. Relative content of different-sized neurons (%)

Ganglia	Large	Medium	Small
Visceral	17.8±1.6	22±1.8	60.2±2.0
Cerebropleural	18.8±1.6	23.2±1.7	60±2.1
Pedal	22.6±1.8	21.0±1.8	54.4±2.2

Three groups of neurons (large, medium and small) are distinguished in the ganglia of the scallop, depending on body size. The nerve cells of each group occupy a certain position. The largest cells are found directly under the membrane of the ganglion; this is followed by a layer of medium-sized neurons; the small neurons are located predominantly at the boundary with the neuropile.

A count of the medium-sized neurons of each group has shown that the largest cells are found in the visceral ganglion (6272±207 μm^3), and the smallest ones (2891±132 μm^3) are found in the cerebropleural ganglia. The volume of the medium neurons is the largest in the visceral ganglion (2406±108 μm^3), and the volume of the small ones is the largest in the pedal ganglia (679±24 μm^3) (Table 2). Small cells predominate (60.2±2.0% in the visceral ganglion). There is a relatively large number of large cells in the pedal ganglia which innervate mainly the muscles of the foot (Table 3).

Unipolar neurons are the most numerous in the ganlia of the scallop. These neurons are most commonly found in groups; their processes coil up in a single bundle and pass into the neuropile. Neurons with two processes issuing from the two opposite poles or the same pole of the cell, as well as multipolar neurons, are far less common. The processes of the latter are sometimes discernible up to the neuropile and, less commonly, in the cortical layer of the ganglion. Similar observations were made by Gubicza and Zs.-Nagy (1965) when studying *Anodonta cygnea*. These authors came to the conclusion that this type of cells is responsible for intra- and interganglial connections.

A basophilic substance is common for the cytoplasm of neurons; its formation and quantity vary in different cells. The small neurons are characterized by a low content of finely granular, sometimes dust-like basophilic substance which is more often uniformly distributed in the cytoplasm. Angular clumps displaced to the margin of the cell are more abundant in large and medium neurons. The scallop has displayed seasonal changes in the content of basophilic substance, which correlates with the secretory cycles in the cell, and apparently reflects the complex cyclic processes in the nervous system (Motavkin, Baraksin, 1983). On the whole, the basophilic substance is found in a dynamic state, and so the ganglia, depending on the degree of basophilia, contain different types of cells at any time of the year.

The endoplasmic reticulum consists of numerous vesicles. Small smooth and rough vesicles measuring 200-400 nm combine with cisternae up to 1 μm in diameter, which contain material of low electron density. The ratio of free and fixed ribosomes varies with the season of the year. As the cytoplasm of the neuron loses the basophilic substance, it is replaced by homoropositive material, solitary and numerous small vacuoles.

A yellow granular pigment is less common in the cytoplasm of the neurons. As we know, such a pigment is formed by elementary bodies called cytosomes. Impregation methods are used with the greatest success to detect neurofibrils in large neurons. The apparatus is formed by a limited number of fairly thick and argyrophilic threads arranged around the nucleus and very densely around the starting point of the axon where the individuality of the neurofibrils becomes difficult to discern. Although the microtubules and filaments in the small neurons are an equally stable cytoplasmic component, the neurofibrils in them cannot be impregnated with silver nitrate.

The cytoplasm in the neurons of the scallop is characterized by tubular mitochondria of spherical shape with a diameter of 0.3-1 mm. Of the other ultrastructural components, we should mention the multivesicular bodies, the primary and secondary lysosomes and the monoaminergic vesicles.

A neuron usually contains one nucleus; binucleate cells are very rare. A fine heterochromatin reticulum is clearly seen in the karyoplasm; some of the chromatin bodies belong to the nuclear membrane. There is one nucleolus, less commonly two of different size, in a central or ectopic position. A peripherally displaced nucleus is noted in cells loaded with inclusions, homoropositive material, lipids, and yellow pigment.

As we have already noted, the neuropile in the Yezo scallop is formed mainly by nerve cell processes, and occupies the central and greater part of the ganglion. The diameter of the cross-sections of the new processes is quite variable (0.1-4 μm). The axons are characterized by typical microtubules, and in some cases they are replaced by thin contorted filaments. The tubular mitochondria with a dense or light-coloured matrix are drawn out in length to 2-3 mm. The matrix of the axon sometimes contains vesicles of the endoplasmic reticulum.

The classification of the axons is based on the structural characteristics of the synaptic vesicles. In the Yezo scallop, the axons of the first group (with a population of agranular vesicles) comprise 25-30% of all the neuropile conductors. The vesicles have a regular spherical or slightly elongated form, and a diameter of 25-70 nm. In some axons, the vesicles are distributed quite uniformly; mostly only individual vesicles are seen in the centre of the axon, whereas a high concentration of them is found near the membrane (Motavkin, Varaksin, 1980). The second group of axons includes two types of granular vesicles, small ones (from 25 to 50 nm) and large ones (160-170 nm). The populations of small vesicles in one, the smaller, part of the axons consist exclusively of small vesicles, while the larger part contains an admixture of large vesicles. A significant number of axons has mostly large granular vesicles. Axons with strictly large granular vesicles are often encountered as well. The third group of neuropile axons contains the typical neurosecretory peptidergic granules with a structure similar to the one known for all animals. Material of different electron density is found in the centre of the elementary granule; it usually has distinct boundaries, and is separated from the membrane by a narrow light-coloured rim. The number of axons with peptidergic granules is subject to seasonal changes, and is related to the sexual activity of the scallop.

The classification of axons by the type of vesicles is relatively reliable. In the neuropile of the ganglia, we often encounter nerve conductors which include almost all the types of vesicles. However, elementary peptidergic granules and transparent or electron-dense vesicles are a particularly frequent combination in an axon.

The main type of neuronal relations in the nervous system of the scallop is the axo-axonal synapse. The most common is the synapse with a heterogeneous population of vesicles in the presynaptic element; it contains small agranular and small or large vesicles with a central or ectopic granule. Another variety of heterogeneous synapse in the presynaptic part contains elementary peptidergic granules with granular or agranular vesicles. Synapses with a homogeneous population of vesicles are less common, and come in three varieties. The first is characterized by the presence of large transparent agranular vesicles grouped near the membrane; the presynaptic element in the second variety has vesicles with a punctate electron-dense granule in the centre; the presynaptic element of the third variety is characterized by large vesicles with an electron-dense centre.

In a number of cases, the elementary types of synapses, by combining, form complex synaptic groups. During synaptic **convergence**, several synaptic profiles with a different or a similar set of synaptic vesicles are found on one or both sides of the postsynaptic axon containing microtubules, neurofilaments and individual mitochondria. During synaptic **divergence**, a presynaptic element with a homogeneous or heterogeneous population of synaptic vesicles interacts simultaneously with 2-3 axons. Synaptic **modification** is observed in the case where three or more axons form a group in which one or several presynaptic buds are at the same time postsynaptic elements. In some cases in the Yezo scallop, we observe typical elementary synapses in which it is difficult to differentiate the presynaptic and postsynaptic elements, since both of the contacting axons have vesicles and a similar differentiation of the elementary membranes. All the types of synaptic complications in the ganglia can be seen on a limited part of the neuropile which sometimes contains up to 10 axonal profiles.

It has been established with certainty that the Yezo scallop is characterized by axonal (axo-axonal) and somatic (axosomatic) localizations of synapses in the neuropile and ganglionic cortex respectively. Two types of elementary synapses have been detected on the perikaryon of large neurons by impregnation methods using a light microscope. The most frequently occurring type of synapse has a presynaptic part in the form of a solitary clavate thickening 10-15 µm in diameter. This type of connection is found on the axonal cone or in the part of the neural soma closest to it. The other, less common, axosomatic connection is quite comparable to the "basket" synapse of the nervous system of vertebrates. A plexus resembling a shallow elongated cup forms on one side of the cell.

Both types of axosomatic synapses are rarely encountered on the neurons of the scallop, either because of their natural scarcity, or because of the inadequacy of the impregnation methods. Since axosomatic contacts are very rarely detected ultrastructurally as well, the assumption regarding their limited occurrence is obviously in full accord with the actual presence of these relations. Axosomatic contacts are very rarely detected in other bivalve mollusks (Zs.-Nagy, 1964). Therefore, the synaptic organization of the nervous system in the Yezo scallop, as in other bivalves, is quite diverse and complex.

4.2. Peptidergic secretion

It has been shown that homoropositive peptidergic cells are found in the cerebropleural, visceral and pedal ganglia of the scallop. The number of inclusions and their morphological makeup in different neurons of the same ganglion vary. Homoropositive material is the most common in medium-sized unipolar neurons, and less common in large ones. When stained with paraldehyde-fuchsin, the cytoplasm of these cells turns light blue. The finely granular dust-like inclusions in this case are uniformly distributed throughout the cytoplasm. Larger granules up to 1 µm are less common. In other neurons, the homoropositive inclusions form perinuclear accumulations, often at one of the poles of the cell. Besides granules, vacuoles are detected in the cytoplasm of some neurons. Their size in the neurons of the visceral ganglion sometimes reaches 5 µm. Along with large vacuoles, the cytoplasm of some cells may contain a significant number of small vesicles 0.5-1 µm in diameter, which are similar or different in colour density.

Ultrastructural studies of secretory homoropositive cells have shown that they have a large number of mitochondria, a well-developed granular endoplasmic reticulum which is usually located along the periphery of the cytoplasm, and Golgi cells. The main characteristic of these elements is that the cytoplasm contains elementary peptidergic neurosecretory granules 120-300 µm in diameter. The number of granules differs; they sometimes occupy a substantial part of the cytoplasm. The central part of the granule is occupied by homogeneous electron-dense material surrounded by a light-coloured submembranous vesicle. Structurally similar elementary granules are observed in the axons.

The different stages in the functioning of the neurosecretory cell have their own characteristic number and morphology of homoropositive inclusions, rate of their synthesis and elimination, as well as morphometric parameters of the secretory cell (Varaksin, 1977). This gives grounds for evaluating the secretory activity of the ganglia of the scallop throughout the year. In spawned-out individuals, a large part of the neurons in the neural ganglia does not contain homoropositive inclusions. The cytoplasm of the cells has a light colour, and some of it contains a few small vacuoles. Homoropositive granules are not found in the neuropile either. A similar cytologic picture is observed in both the females and males of the scallop throughout the second half of June-August.

In September—October, homoropositive material appears in some of the secretory neurons of the ganglia in the males and the females. A small number of inclusions is noted in the neuropile. The cells, nuclei and nucleoli increase in volume. The nuclear-plasmic relations also increase. The cells attain their highest volume in October. The number of neurons at different stages of secretory activity increases, and, as an example, reaches 64% in the cerebropleural ganglia of the female (Fig. 17). In the greater part of these cells, the granular inclusions occupy a perinuclear position. The size of the granules does not exceed 0.5-1 µm. Homoropositive material is detected in the axons, and is seen throughout the observable length of the neural conductor. In winter, secretory activity diminishes in both the males and females (Fig. 18). This process is characterized by a decrease in the number of secretory neurons and their volumes; homoropositive inclusions are rarely detected in the axons.

The secretory processes in the ganglia are reactivated beginning in February. A significant increase is noted in the size of the body, the nuclei and nucleoli of the neurons and the number of secretory neurons at different stages of the secretory cycle. The nucleus/plasma ratios increase, reaching their maximum values in the neurons of the cerebropleural ganglion of the female. A marked change in the cytologic patterns and morphometric indices in the neurons of the ganglia is noted shortly before spawning. The number of secretory cells and cytoplasmic inclusions decreases, and their morphological makeup changes. A large number of homoropositive granules appears in the axons, which is an indication of mass eliminatiion of secretory inclusions from the neurons.

One can say that a large portion of the neurons in the Yezo scallop is capable of producing homoropositive peptidergic material. Throughout the year, two peaks of secretory activity are observed in the ganglia of the scallop, the first in October—November, and the second in March—April. The abundance of secretory cells changes. The amount of secretory material and its morphological makeup do not remain constant either. Particularly significant changes in secretory activity are observed in the cerebropleural and visceral ganglia, and the activity of these ganglia throughout the year in the males and females changes synchronously to a large extent.

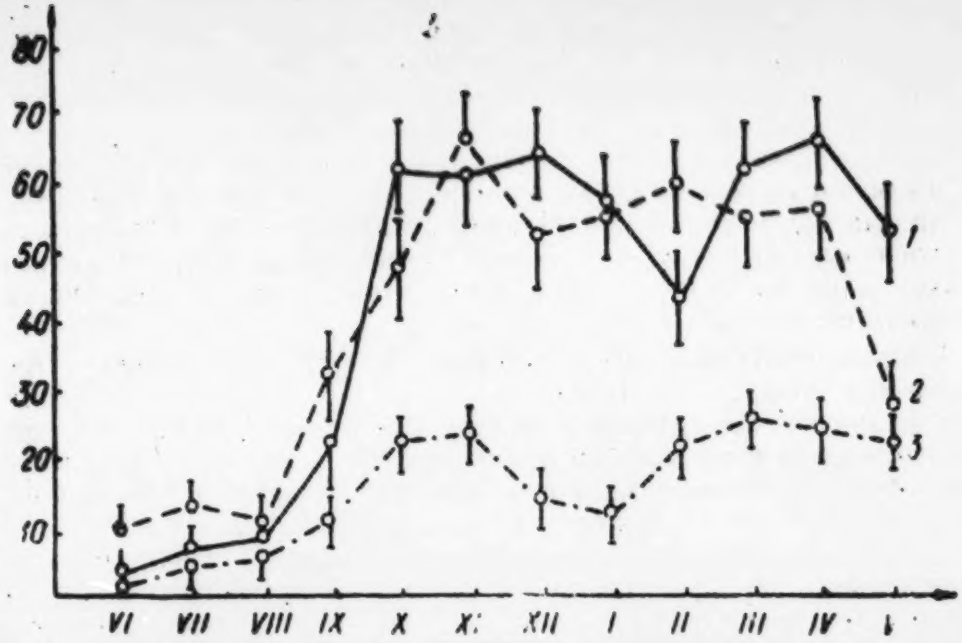


Fig. 17. Change in the content of secretory neurons in the ganglia of the females of the Yezo scallop throughout the year. Here and in Fig. 18: X-axis - months; Y-axis - percentage of secretory cells; 1 - cerebropleural ganglia, 2 - visceral ganglion, 3 - pedal ganglia

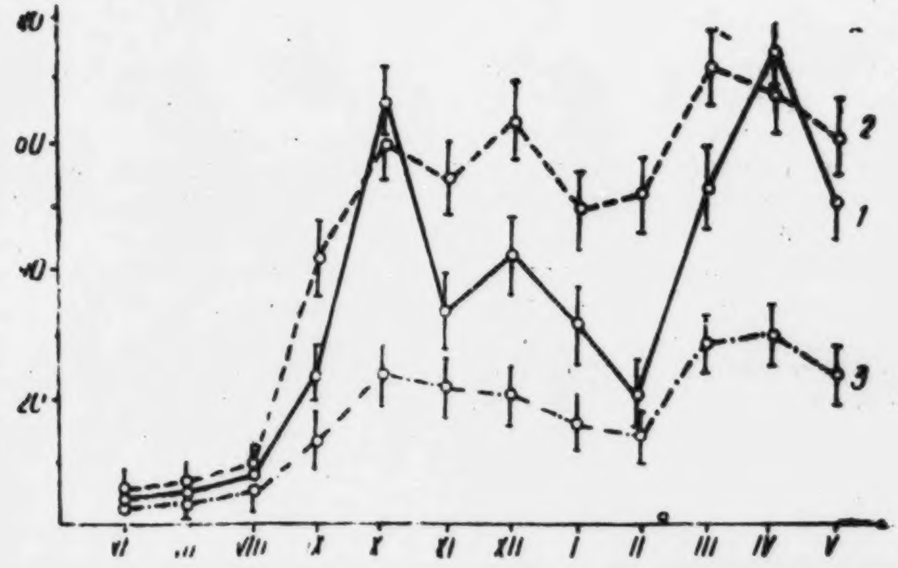


Fig. 18. Change in the percentage of secretory neurons in the ganglia of the male of the Yezo scallop throughout the year

4.3. Cholinergic neurons

As we know, acetylcholine esterase, an enzyme that inactivates excreted acetylcholine, is distributed quite unevenly in the nervous system. This type of localization of choline esterases is also characteristic of the ganglia of the Yezo scallop. The precipitates of copper sulphide, the end product of a histochemical reaction, form clearly defined loci of different size and shape. The focal nature of distribution of the precipitate in the neuropile allows us to assume that the activity of acetylcholine esterase is confined mainly to the synaptic regions. The activity of the enzyme is low in the neural conductors; on the other hand, acetylcholine esterase is not detected in the perikaryons.

It is currently believed that the study of cholinacetyl transferase, an enzyme that takes part in the synthesis of acetylcholine and is localized mainly in the membranes of the synaptic vesicles, will open new possibilities in the diagnosis of the cholinergic functions of the neuron. In marine invertebrates, the distribution of cholinacetyl transferase in the nervous system has been studied only in some species. In the nervous system of the Yezo scallop, the enzyme is detected in the perikaryon, sometimes at the starting point of the axon. The precipitate that forms varies in density and colour; it may have a granular or homogeneous structure, local or diffuse distribution in the cytoplasm. Three types of neurons are distinguished in accordance with these characteristics.

The first type of cells contains a homogeneous yellow or light brown precipitate uniformly distributed in the cytoplasm; small granules and lumps are occasionally noted. In cells of the second type, the precipitate is found around the nucleus; it has a dark brown colour and a homogeneous or granular structure. Neurons of the third type contain the highest amount of precipitate; the latter occupies all of the cytoplasm, has a lumpy or granular structure, and is dark brown. The massive nature of the precipitate and its colour allow us to form an opinion regarding the activity of cholinacetyl transferase, but since the latter is a variable value and undoubtedly related to the functional state of the neuron, the given types characterize the ephemeral stage of the cell and can be encountered in the ganglia of the scallop in the most diverse combinations. Among the reactive, basically unipolar, neurons, we often encounter multipolar cells with a finely granular precipitate in the initial segments of the processes.

Thus, the enzymes of acetylcholine metabolism in the Yezo scallop are detected in different parts of the neuron, acetylcholine esterase predominantly in the neuropile, and cholinacetyl transferase exclusively in the perikaryons.

4.4. Aminergic neurons

Biogenic amines, like the transmitters of nerve impulses, are widespread in the nervous system of bivalve mollusks. Histochemical fluorescence-microscopic methods have helped to establish that the localization of biogenic monoamines in the Yezo scallop is similar to that in other mollusks. Cellular bodies give off an intensive glow in the cortical layer, and fibres and sometimes terminals luminesce in the neuropile. The overwhelming majority of the neurons are yellowish-green, sometimes with a golden luminescence. A smaller part of the cellular bodies glow emerald green, similar to the axons and terminals in the neuropile. According to the generally accepted point of view, the yellow luminescence is cause by serotonin, and the green by catecholamines, which is consistent with the biochemical assays of biogenic amines in bivalve mollusks.

Histochemical analyses of monoamine oxidase, an enzyme participating in the oxidative deamination of catecholamines and serotonin, have shown that most of the neurons of the ganglion show a slightly positive reaction; a bluish, finely granular or diffuse colour is observed in their cytoplasm.

Therefore, two main monoaminergic systems exist in the Yezo scallop, as in the other bivalves studied to date, a system with dophamine, and one with serotonin. An insignificant part of the neurons can apparently synthesize and deposit noradrenaline, as indicated by biochemical data; however, it is difficult to identify them by means of fluorescence microscopy.

4.5. Peripheral nervous system

The peripheral nervous system of the Yezo scallop has not been researched as well as the central nervous system. The available data relate mainly to the innervation of the gonad; similar data are not available for the other organs. The sources of gonadal innervation in the scallop have not been established with certainty; we have only indirect data that the main region contributing to the formation of the nervous system of the gonad is the visceral ganglion and, apparently, the small nerves arising in the cerebrovisceral connective. The nerve elements are distributed in the wall of the gonad, and only some of the terminal elements reach the acini.

Before entering the wall of the gonad, the nerves divide into thinner ramuli, and run independently or along the course of the hemolymphatic vessels, repeating their divisions. The intramural nerves can be divided quite arbitrarily into vascular and tissue nerves, which extensively exchange fibres with each other. As a result, an anatomically and functionally unified neuroplexus is formed. Three regions are differentiated in it, namely the outer subepithelial region which forms mainly the sensory receptors, the middle muscular-connective tissue region, and the deep subgerminal region represented by a limited number of axons.

The middle region is the most developed and structurally complex. It contains the largest nerves which measure up to 30 μm in diameter. An extensive meshwork of individual fibres and fine neural conductors forms between them. Some ramuli come up to the basement membrane of the multirow ciliated epithelium that covers the wall of the gonad. Here, amidst the connective tissue, they break down into fibres, and form a sparse network of nerves. The other group of thin nerve ramuli and individual axons arising from the same nerves forms the subgerminal region.

In addition to the neural conductors, nerve cells are encountered in the wall of the gonad, mainly in the subepithelial layer. Most commonly, they are arranged one by one, but sometimes they form groups of a few neurons. These observations are not unexpected. For example, bipolar neurons have been described in the subepithelial neuroplexus of the intestine of *Anodonta cellensis*, and unipolar neurons in the epithelial layer (Gilev, 1952). Unipolar and multipolar neurons with highly osmiophilic cytoplasm have been found in the connective tissue of the anterior byssal retractor of *Mytilus edulis* (Bowden, Lowy, 1955; Gilloteaux, 1972).

The use of Falk's histochemical fluorescent-microscopic method has shown that the cytoplasm of neurons has yellowish-green fluorescence; however, it is difficult to say which of the biogenic amines are contained in this or that cell. There is also no clear answer as to which functions are carried out by these neurons. It is quite probable that the sensory function is performed by the bipolar neurons. Protoneurons are widely distributed in invertebrates, and therefore it is not excluded that cells of this type are present in the wall of the gonad in the scallop. However, some of the intramural neurons apparently perform an excitatory function.

When dense and extensive neuroplexi are present in the wall of the gonad, the terminals characteristic of the sensory organs are quite rare. In some cases, we managed to detect them by supravital staining with methylene blue. However, the sensory terminals are detected to the fullest extent by Koelle's method with prolonged incubation of specimens. Analysis of whole-mount specimens has made it possible to establish in greater detail the structure of the receptors and the innervation by them of certain histological elements, which is very rarely achieved with histological sections. The pattern of formation of the receptors is quite simple; as the axon begins to divide, it produces a number of ramuli which undergo further, mostly dichotomous, division. This results in the formation of fairly uniform dendroid endings which differ in the number and density of distribution of the terminal ramuli. The structure in which a fibre forms 2-3 terminals can be regarded as an elementary receptor. The structure of complex receptors depends on the number of axonal divisions and the size of the area occupied by them. The more a fibre divides, the denser the ending becomes and the more complex it appears.

When the wall of the gonad was subjected to supravital staining with methylene blue, receptors with a more diverse structure (terminal endings thickened and often expanded) were detected. Apparently, this is due to the fact that methylene blue detects other, more complex receptors, or, because of a certain degree of toxicity, alters the structure of the terminals drastically. The sensory terminals are concentrated mainly in the muscular-connective tissue layer of the gonad; fewer sensory endings are detected in the subepithelial layer adjacent to the basement membrane. The sparsely branching terminals are usually seen in many fields of vision, and innervate large areas. Since myocytes and intercellular collagen-like fibres form a single musculotendinous organ (Varaksin, Deridovich, 1984), it is likely that all or a large part of the sensory endings of this layer of the gonad can act as mechanoreceptors . The gonadal epithelium of the scallop comes into contact with the environment, and is not an absolutely impermeable barrier, but sooner a selectively permeable one for a number of substances dissolved in the water, to which subbasal receptors may be sensitive.

The presence of various mediator mechanisms is a prerequisite for the functioning of the nervous system in the wall of the gonad. However, there is very little information on the histochemical identification of axons in the gonad of the Yezo scallop (Varaksin, 1980). The monoaminergic nervous system is detected in the form of a dense network of fibres luminescing mostly with a yellowish-green, less commonly green, light. Considering the nature of the luminescence, one can assume that the greater part of the conductors contains serotonin, and the smaller part dophamine. This assumption is confirmed by biochemical data. For example, with the use of a microfluorimetric method, it was shown that the content of serotonin in the wall of the male gonad amounts to 4.6±0.2 μm/g of fresh tissue, that of dophamine 3.5 times less than serotonin (1.3±0.1 μm/g), and that of noradrenaline more than 10 times less than serotonin (0.40±0.02 μm/g).

The juvenile and sexually mature scallops differ significantly in the structure of the monoaminergic nerves. In the gonad of juveniles, we observe a finely structured network of monoaminergic axons with the biogenic amines concentrated in the ganglia of this network. In sexually mature scallops, the axons are gathered in thick, brightly lumininescing bundles. The monoamines are formed in rough angular lumps which can be seen along the entire length of the nerve fibre. In the sexually mature individuals, we note a certain seasonal variability in the content of biogenic amines in the gonadal wall, which is apparently due to the cyclic changes in the gonad.

The histological methods currently available limit the detection of cholinergic fibres. It is impossible to mark the cholinergic elements with the help of a specific histochemical method for detecting the enzyme of acetylcholine synthesis, cholinacetyl transferase, since the enzyme is found in the axons in a highly active soluble form. The cholinergic function of the neural conductors was determined by the distribution of acetylcholine esterase, detected by Koelle's method with the peculiarities of the method taken into account, which made it possible to differentiate the cholinergic elements from the cholinoceptive ones.

Analysis of whole-mount preparations of the gonadal wall after brief incubation (1-1.5 h) and prolonged incubation (up to 20 h) in a medium showed different results. In the first case, we noted a very sparse network of highly perceptible axons without the terminals characteristic of receptors. Such cholinergic axons are undoubtedly found predominantly amidst the muscle cells of the gonad. With prolonged incubation, the network of fibres becomes denser, and the typical receptors, nerve fibres and nerve bundles appear in all the layers of the muscular-connective tissue membrane.

Optical morphological and histochemical observations provide more extensive and more detailed data on ultrastructure. The individual nerve fibres and thin bundles seen under a light microcope actually represent complexes of axons with different functions, if the latter are judged on the basis of the type of vesicles contained in them. The nerve bundles are separated from the connective tissue by a discontinuous glial membrane. The processes of the gliocytes penetrate the bundle, but do not form a continuous cover around the individual axons. The axons, which measure over 3 µm in diameter, are solitary. In thick axons, we can usually see filaments, microtubules and, more commonly than in thin axons, mitochondria. On the other hand, specific synaptic vesicles are almost always detected in the thin axons. In the pre-terminal and terminal regions, the number of axons decreases to several. Most of the nerves are concentrated in the muscular-connective tissue layer, where different types of vesicle-containing axons can be seen. As in the neuropile of the ganglia, conductors with an array of homogeneous and heterogeneous vesicles are present here.

The presence of axons with elementary peptidergic granules in the wall of the gonad is of special interest. Peptidergic granules differing in size and abundance are detected in axonal profiles of different size. The density of the granules varies from translucent with an illegible structure to typical with an electron-dense centre surrounded by a light-coloured rim (Varaksis, 1980). The structure of the granules apparently changes as material is secreted into the surrounding tissue of the organ. In this case, the residual bodies have the form of a vesicle with a clearly contoureed membrane and electron-transparent material. The pre-terminal and terminal regions of the axons are often found amidst the collagen-like fibres near the muscle cells, and in some cases lie almost adjacent to them. Another group of axonal profiles includes monoaminergic synaptic vesicles with a dense centre. Transparent vesicles, apparently with acetylcholine, are far less common in the profiles of the axons. Specialized neuromuscular contacts were not observed, though, in some cases, terminal varicosities with granular vesicles were found at a distance of 30-50 nm from the membrane of the muscle elements.

One can conclude that the nervous system of the gonad in the Yezo scallop contains intramural neurons, as well as peptidergic, cholinergic and monoaminergic axons. In excitatory innervation of the gonad, greater significance is attached to the monoaminergic appartus; in any case, cholinergic innervation involves a much smaller number of axons. The peptidergic elements apparently play an important role in effecting the gonadal functions of the nervous system.

5. SENSORY ORGANS

The general organization of the sensory system of bivalve mollusks has a number of characteristics which distinguish them from other animals of this type. In the majority of mollusks, the organs of sight, equilibrium, chemical and tactile sensitivity are concentrated in the anterior region of the body. Sensory information from these organs is sent to the cerebropleural ganglion. In bivalve mollusks, a sedentary mode of life and passive feeding have brought on a displacement of the sensory organs (except for the organs of equilibrium) towards the edge of the mantle which comes into direct contact with the environment. The function of the main centre for the processing of sensory information was taken on by the visceral ganglion.

Among the bivalve mollusks, the members of the Pectinidae are characterized by the most complex and diverse forms of behavior, achieved through a relatively high level of development of the sensory organs. Because of this, the receptors of this family have served as the subject of study more frequently than those of other species of bivalves. However, it should be said that the extent of the research into the sensory systems of the bivalves, specifically the Pectinidae, is still insignificant. The research into the sense organs of the Yezo scallop is only beginning. For example, the literature is practically devoid of information on the structure and functional characteristics of the organs of equilibrium (statocysts, organs of sight and chemical sensitivity). Some progress has lately been made in the study of mechanoreception, the capacity of an animal to react to tactile and vibrational stimuli. Structures found along the edge of the mantle and the abdominal sense organ are responsible for these types of sensitivity in the Yezo scallop.

Considering the fact that the sensory systems of the Yezo scallop have been poorly researched, in the cases where data on the structure of this or that sense organ is not available, it would be worthwhile to give a brief description of the corresponding structures of similar species. This approach has to do with the fact that the sense organs within a family differ insignificantly both in their morphological and functional characterisitcs (Franc, 1960; Charles, 1966; Frenkiel, 1980).

5.1. Organs of sight

The organs of sight in the Yezo scallop consist of specialized structures, ocelli, which are found on the ocular tentacles of the mantle margin. There are 80 of these ocelli on the average. They are evenly distributed along the perimenter of the mantle margin, there being more ocelli on the left side of the body, than on the right.

A comparative study of the structure of the ocular tentacles in some species of the genera *Chlamys, Ammussium* and *Spondylus* (Dakin, 1928) did not reveal any differences in the morphology of the organs of sight. Investigations have shown that the ocelli of pectinids have a cornea, a crystalline lens, a double retina formed by a distal and a proximal layer of photosensitive cells, a reflecting layer (argenteum), and a pigmentary layer. Electron-microscopic examination of the eyes of *Pecten maximus* (Barber et al., 1967) has shown that the distal retina is formed by ciliated cells, the cilia of which have a 9+0 set of axonemes. The nerve process of the cells of the distal retina branches out in a somewhat unusual place, from the area covered with cilia. The proximal layer of the retina is formed by microvillous rod-shaped cells. The axon of these cells arises from the part devoid of microvillae. The axons of the proximal and the distal retina go partly into the circular mantle nerve, but mostly run directly as part of the radial nerve into the visceral ganglion. The glial cells are included in the retina along with the photoreceptor cells. The reflecting layer (argenteum) is formed by cells with regular alternation of cytoplasmic areas and guanine crystals which form a multilayered concave mirror. The cells of the pigmentary layer form the outer membrane of the eye. In Land's opinion, the structure of the eye in pectinids contributes to a somewhat deformed image on the distal retina (Land, 1965).

A distinctive feature of the organs of sight in pectinids is the presence of rod-shaped photosensitive cells which form the proximal retina. In the rest of the bivalve families in which the ultrastructure of the organs of sight is known, the retina is formed exclusively by ciliated photoreceptor cells (Barber, Wright, 1969; P. Levi, C. Levi, 1971).

Electrophysiological experiments, in which the reaction of *Placopecten magellanicus* to light was studied, have shown that the photosensitive cells of the distal retina react with a spurt of impulse activity when light is switched off (on-response). On the other hand, the photoreceptor cells of the proximal retina are stimulated when light is switched on (off-response) (Hartline, Graham, 1938; Land, 1966). The intracellular registration of the receptory potential has shown that the changes in the impulse response are determined by the development of the receptory potential arising in response to the change in light intensity in the cells of the distal and the proximal retina (McReynolds, Gorman, 1970). In the cells of the distal retina, a hyperpolarization (inhibitory) receptory potential develops in response to illumination; it is replaced by a depolarization (excitation) potential when the light is switched off. The opposite changes in potential are observed in the cells of the proximal retina, i.e. depolarization when the light is switched on, and hyperpolarization when the light is switched off.

In studies conducted with the Yezo scallop, we also observed impulse activity changes in the radial mantle nerve in response to light intensity changes. At the same time, an increase in pulsation frequency was noted in response to both the switching on and the switching off of the light. The intensity of the reaction was determined by two parameters of the light stimulus, its duration and its intensity. For example, the impulse frequency in the off-response was proportional to the duration of the preceding light adaptation, while the value of the on-response was determined by the intensity of the light.

These data indicate that the optical system of the Pectinidae is distinguished by a high level of specialization, which is reflected in the structure of the ocular tentacles and their functional characteristics. This is apparently due to the active mode of life of the scallop. The high level of development of the optic system can play an important role in its biology, primarily in the detection of predators or during migrations.

5.2. Tentacles of the mantle margin

Along the entire perimeter of the mantle edge of the Yezo scallop, we find numerous pallial tentacles which clearly fall into three size groups, short, medium and long.

The short tentacles, which are relatively scarce, are distributed along the margin of the velum, and are slightly coniform. When extended, they do not exceed 10 mm in length. When touched lightly, the short tentacles contract, and in this state do not exceed 2-3 mm in length. A study of the short tentacles with the help of a scanning electron microscope has shown that their surface is covered with tubercular processes (Fig. 19). The tops and sides of these tubercles bear small pits from which bundles of cilia extend. Proceeding from the fact that the short tentacles are sensitive to the effect of mechanical factors, one can assume that the ciliated cells of the tubercles are receptors.

The medium tentacles are the most abundant. In the Yezo scallop, they are found near the periostracum along the perimeter of the mantle fold. The contractibility of these tentacles is comparatively low. Their length in mature individuals varies from 10 to 15 mm. When observing live specimens with the help of a light microscope, we can see that the entire surface of the medium tentacles is covered with motile cilia, the beating of which creates an intense current of water from the base to the apex of the tentacles. Because of the movement of the cilia, the medium tentacles, found at some distance from the mantle, can move forward on their base along a smooth bottom. Touching causes a slight contraction of these tentacles, which points to the presence of mechanoreceptors on their surfaces.

The long tentacles of the mantle margin are found in the spaces between the ocular tentacles. They are highly motile and contractile, and can extend from 5-7 mm to 60 mm. Many researchers have noted the sensory function of this type of tentacles in the Pectinidae (Charles, 1966; Frenkiel, 1980). Back in 1909, Dakin showed that the long tentacles of the mantle margin of the scallop bear ciliated receptor cells which are connected to the nerve network. According to the data obtained with the help of a scanning electron microscope, the long pallial tentacles of the Yezo scallop are 1/3 covered with papillate processes (papillae) 15-20 μm in diameter and 80-140 μm in length . The apex of the papillae bears a bundle of short cilia 3-5 μm long. Bundles of short cilia are also present at the base of some papillae. The rest of the tentacle (about 2/3 of its length) is devoid of papillae, and has a plicate surface with relatively sparsely distributed cells bearing a bundle of short (4-8 μm) cilia.

When examined under a light microscope, sections of the apex of a long tentacle showed that the nerve trunk passes through the centre of the cylindrical tentacle. Around it lies a layer of muscle fibres and connective tissue, surrounded by a basement membrane. When longitudinal sections through a papilla are examined, a group of cells topped with a bundle of cilia oriented at a 90° angle to the long axis of the tentacle is noted in its central part.

The papillae are formed by two types of cells (Fig. 20).

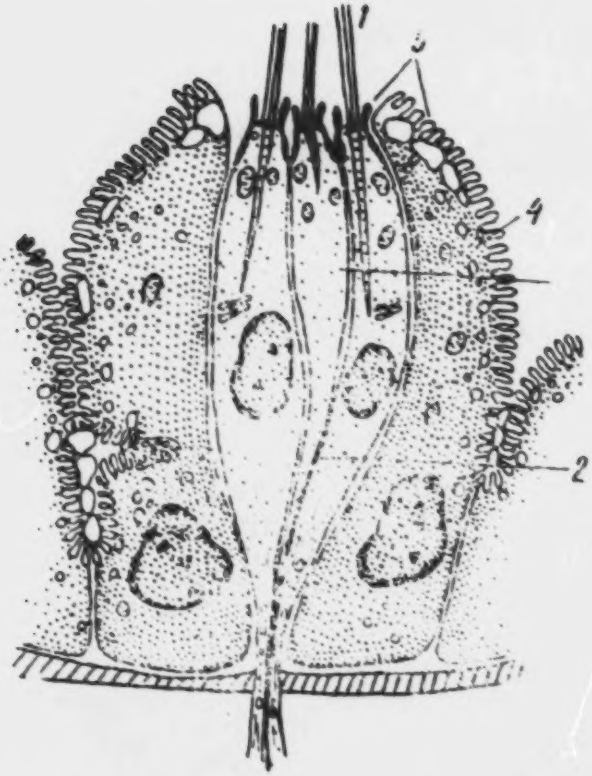


Fig. 20. Structure of the epithelial papilla of the long tentacle in the Yezo scallop: 1 - cilia; 2 - roots of cilia; 3 - ciliated cells; 4 - microvillous cells; 5 - microvillae

The cells of the first type are microvillous, 30-35 μm in length and 5-7 μm in diameter, and they form the capsule of the papilla. They have an electron-dense cytoplasm in which numerous vacuoles and granules of different size are seen amidst the usual inclusions. The free surface of these cells is covered with a multitude of microvillae. The space between the microvillae is filled with electron-dense granular material, probably of a mucopolysaccharide nature. The morphological characteristics of the first type of cells, as well as the absence of cilia in them permit us to regard them as supporting elements. The same conclusion was reached by Moir

(1977a) who studied the structure of the papillae in *Placopecten magellancius*.

The cells of the second type are ciliated, located inside the capsule, and have the spindle-like shape typical of receptor cells. They measure 25-30 µm in length, and their diameter in the widest part does not exceed 5 µm, and in the apical part 0.6-0.8 µm. The cytoplasm of the second type of cells has the usual cellular inclusions, and in electron-diffraction diagrams appears lighter than the cytoplasm of the first type of cells. The narrow apical part of the ciliated cells appears on the surface of the apex of the papilla. They are surrounded by a ring of microvillae. The cilia are 3-5 µm long. The internal structure of the cilia is defined by the usual fibrillary formula 9+2. The fibrils arise from the basal pedicle. The roots of the cilia are very long, and almost reach the nucleus. Analysis of numerous electron-diffraction diagrams of the basal parts of the papillary cells shows that some of them have outgrowths that penetrate deep into the tentacle. The characteristics of the ciliated cells, which indicate that they belong to the receptor cells, give grounds for assuming that namely these cells have a neural process and are protoneurons. This view is consistent with Moir's data (Moir 1977a) which notes the presence of a structure practically identical to the tentacular papillae of the Yezo scallop on the end of the long tentacles of *P. magellanicus*. This author also concludes that the cells of the second type are of a receptory nature, though he did not manage to establish a direct relation between these cells and the tentacular nerve, as Dakin had done (Dakin, 1909).

According to Moir, the ciliated cells at the base of the papillae have an oval form and a diameter of about 10 µm. The apical surface of these cells, along with numerous cilia, bears a macrocilium formed of 2-9 cilia united by a common cellular membrane.

Electrophysiological experiments have shown that the entire surface of the mantle margin in the Yezo scallop is highly sensitive to mechanical stimuli (Zhadan et al., 1980). A light touch of a thin needle to the tip of the long tentacle produced two effects at the same time, an impulse discharge in the radial pallial nerve and contraction of the tentacle. With an increase in the intensity of the stimulus, the frequency and duration of the impulse reaction increased, and adjacent tentacles became involved in the contraction process. A similar reaction was observed with mechanical stimulation of the medium and short tentacles, as well as the surface of the velum. With high intensities of mechanical stimulation, the contraction wave took in not only the tentacles, but also the surface of the velum. At the same time, the length of the impulse discharge in the radial pallial nerve always exceeded the time of exposure to the stimulus, and often coincided with the duration of the contraction wave. This peculiarity of the response is probably associated with the fact that the process of contraction is a factor which, as it develops, induces the stimulation of the mechanoreceptors, which leads to the lengthening of the impulse discharge in the pallial nerve. When the impulse activity was discharged directly from a single nerve fibre innervating the long tentacles, the impulse response was a short impulse discharge arising synchronously with the mechanical stimulus.

The responses of the mechanoreceptors of the mantle margin were characterized by comparatively rapid adaptation to a constant stimulus and periodically recurrent ones. For example, a touch of a glass stick to the velar region at first induced a high-frequency impulse discharge, followed by a gradual decline of impulse frequency. Removal of the stimulus was followed by a spurt of impulse activity as well. For each subsequent mechanical stimulus, there was a response of a lower impulse frequency than the preceding one in the radial pallial nerve.

The sensitivity to mechanical stimulation of all the surface areas of the mantle margin, including all the types of tentacles, was studied in electrophysiological experiments on other species of pectinids (Stephens, 1978a, c). However, these investigations were carried out with discharge of impulse activity from whole nerve fibres, which does not tell us which of the above-described morphological types of receptor cells are mechanoreceptor cells.

In addition to the sensitivity of the mantle margin to mechanical stimuli, the electrophysiological experiments have demonstrated the sensitivity of this region to chemical stimuli. Experiments performed on isolated long tentacles from the Yezo scallop have shown that perfusion of the tentacle by sea water from an aquarium holding starfish causes an increase in the frequency of impulse activity in the tentacular nerve (Karpenko, 1981). These data point to the presence of chemoreceptor cells that react to starfish scent in the epithelium of the long tentacles. Less informative in this respect are the experiments undertaken by a number of authors who used diluted tissue extracts of starfish and other animals as stimuli (Stephens, 1978a; Zhadan et al., 1980). In these experiments performed on *Aequipecten irradians* and *M. yessoensis*, the authors also managed to record an impulse reaction in the nerve innervating the mantle margin in response to highly diluted extracts from the tissues of various species of starfish, sea-urchins and trepangs. However, when analyzing this type of data, we must take into account that the extracts from the surface tissues of these species contain surface-active substances which can induce a nonspecific response in various nerve cells, including mechanoreceptor cells. This circumstance has been clearly illustrated in experiments where the impulse reaction was recorded in the same nerve fibres in response to both mechanical stimuli and an extract from the surface tissues of starfish (Zhadan et al., 1980).

5.3. Organs of equilibrium

Organs of equilibrium, statocysts, are present in all mollusks. At the initial stage of research, these structures were said to have the function of sound perception, which is why they were initially called otic vesicles (Sokolov, Kovalev, 1979). However, the results of electrophysiological experiments have shown that these organs control the spatial position of the body in relation to the force of gravity.

The structure of the statocysts hardly differs at all in the representatives of different families of bivalve mollusks. They consist of two small hollow spheres which are connected to the mantle cavity by means of a special canal. The cavity of a statocyst is filled with fluid, and contains numerous (about 1 μm) mineral inclusions of endogenous origin, statoconia. The wall of the statocyst is formed by 1-row epithelium composed of alternating receptory and secretory hair cells. Axons that form statonerves extend from the proximal part of the receptor cells. The fibres of the statonerve end in the cerebral ganglion. According to the data of electron-microscopic studies, the sensory epithelium of the statocyst of *P. maximus* contains two types of receptor cells which differ in the structure of the ciliary apparatus (Barber, Dilly, 1969). In some cells, the apical surface bears up to 30 cilia, the basal pedicles of which are parallel to each other. This type of organization of the ciliary apparatus suggests that these cells are sensitive to the direction of the stimulation. On the other hand, the cells of the second type have 9-10 cilia with the basal pedicles directed towards the centre of the cells. These cells are not capable of selectively reacting to any direction of stimulation. The presence of receptor cells capable of sensing the direction of stimulation is the distinguishing feature of the statocysts of pectinids (Frenkiel, 1980). The slow-moving burrowing forms of bivalve mollusks, e.g. *Scrobicularia plana* and *Tellina tenuis*, have receptor cells with only radial symmetry of the ciliary apparatus, which do not sense the direction of stimulation (Frenkiel, Moueza, 1982).

The second distinguishing feature of the organs of equilibrium in the scallop is the asymmetry of their structure. The left statocyst has a larger size and a more complex morphological organization compared with the right one. It is significant that the morphological differences between the right and the left statocyst are clearly correlated with their different functional importance. For example, the removal of the right statocyst has practically no effect on the capacity of *P. inelexus* to move about (Buddenbrok, 1911). At the same time, the removal of the left (larger) statocyst was followed by deterioration of the swimming capabilities of the animal.

No electrophysiological research of bivalve statocysts has been conducted so far. Their functioning mechanism can be judged only on the basis of the structural similarities of these organs in bivalve and gastropod mollusks, since the functional characteristics of gastropod statocysts have been studied in detail (Alkon, Bak, 1973; Gallin, Wiederhold, 1977, etc.). In the studies conducted on species of this class of mollusks, it was established that the animals receive body position/force of gravity information because the statoconia charge the receptor hair cells, inducing an impulse activity higher than in the uncharged cells. The movement of the body relative to the direction of the force of gravity results in the displacement of the statoconia to another part of the statocyst and the stimulation of the corresponding receptor cells. This, in turn, leads to changes in the bioelectric activity of the latter.

Morphological and functional studies of the organs of equilibrium have not been conducted in the Yezo scallop. However, one can expect that the indicated structural features of pectinid statocysts (lateral asymmetry, etc.) are also characteristic of the statocysts of the Yezo scallop.

5.4. Osphradium

The osphradium of mollusks is traditionally regarded as a chemoreceptor (Bullock, Horridge, 1965). This view regarding the function of this organ was based on the data obtained in experiments on gastropods.

The literature contains only fragmentary data on the structure of the osphradium in marine bivalves, data obtained with the help of a light microscope. In pectinids, the osphradium is located at the base of the gills, longitudinally to the branchial nerve. It contains cylindrical ciliated cells and bipolar neurons. The axons of both types of cells enter into the composition of the branchial nerve, and are directed into the visceral ganglion (Setna, 1930). The function of the osphradium in bivalve mollusks has not been established. The osphradium is found on the route of the main flow of fluid from the mantle cavity. This fluid contains the end products of metabolism being washed out of the mantle cavity and gills, as well as kidney excretions, carbonic acid, ammonium hydroxide, inorganic salts, and products of nonprotein metabolism. Therefore, one can assume that the osphradium in bivalve mollusks is also a chemoreceptory organ which contributes to the regulation of metabolism. Electrophysiological studies carried out with freshwater species *Unio pectorum* and *Anodonta cygnea* have shown that the osphradium is sensitive to chemicals such as potassium chloride, ammonium hydroxide, mannitol and glucose (Sokolov, Zaitseva, 1982).

5.5. Abdominal sensory organ

The abdominal sense organ was first described by German researchers (Eisig, 1887; Theile, 1889). Morphological studies of the abdominal sense organ by methods of electron microscopy have been carried out with scallops of the species *P. magellanicus* (Moir, 1977b) and *M. yessoensis* (Zhadan et al., 1982). The function of this organ was established in recent behavioral and electrophysiological experiments on the Yezo scallop (Zhadan et al., 1982). The studies showed that the abdominal sense organ was highly sensitive to vibrations in the water. This organ is an unpaired structure, and is located in the mantle cavity on the right side of the anal aperture, on a connective-tissue ridge formed by a fold of the right mantle to which the organ is attached by a thin strip of tissue. The abdominal organ has the form of a banana. It reaches a length of 3.5-4 mm and a width of 1-1.5 mm in a scallop with a shell diameter of 15-18 cm. Its surface is covered with cilia up to 120 µm in length. The cilia appear motionless when viewed under a light microscope. Under the same conditions of observation, the shorter cilia on the band of tissue at the base of the organ are seen clearly.

The abdominal organ is innervated by two branches of the posterior pallial nerve, which arise in the visceral ganglion. The right branch approaches the organ from the side of the adductor, while the left branch lies closer to the mantle. The right branch of the nerve is 2-4 times thicker than the left one. Directly near the organ, both branches of the nerve split into separate ramuli which run parallel to the long axis of the organ. They send out radial bundles of nerve fibres which end in the epithelium of the organ (Fig. 21).

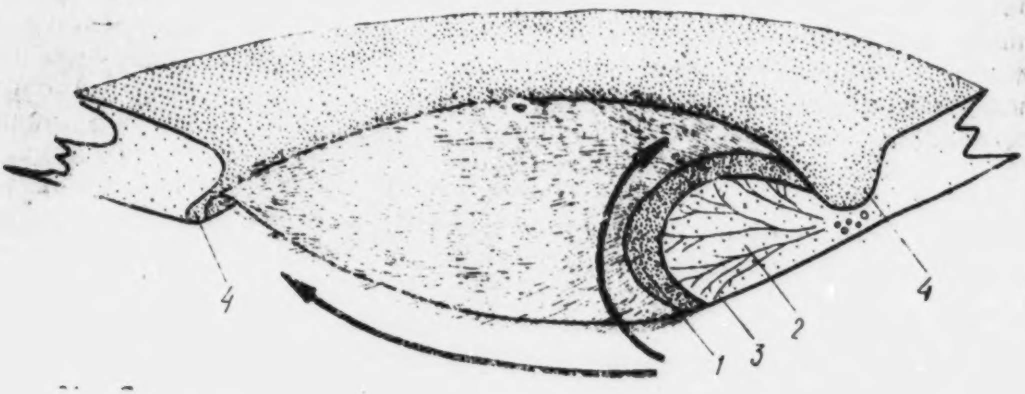


Fig. 21. Abdominal sense organ in the Yezo scallop. 1 - sensory epithelium, 2 - nucleus of organ, 3 - nerve branchings of abdominal organ, 4 - band of tissue

The epithelium of the abdominal organ is multirow. The basement membrane separates it from the nucleus of the organ which is filled with loose connective tissue. Several types of cells are found in the epithelium (Fig. 22). Receptor cells of the first type are most commonly encountered in the epithelium. These are bipolar spindle-shaped cells about 30 μm in length. A peripheral 0.6 μm process connects the cell body with the surface of the epithelium, and bears a single cilium which is surrounded by a double ring of microvillae. The internal structure of the cilium is defined by the fibrillary formula 9+2. The fibrils of the cilium arise from the basal bodies that form the basal pedicles. The primitively striated rootlets of the cilia almost reach the nucleus, and branch vigorously as they penetrate the cell. In cross-sections through the apical region of the receptor cells, we see that the cilia are arranged in a staggered fashion at an equal distance from each other. At the same time, the axes of symmetry of the central axonemes of adjacent rows of cilia are parallel to each other. The length of the cilia in the first type of receptor cells varies in different parts of the organ, decreasing from the centre of the organ to its periphery. A cilium is usually 150-200 nm thick, except for its tip which is bean-shaped and has a diameter 3 times greater than that of the cilium. At the point where the latter thickens, there is a number of slightly granular vacuoles measuring from 20 to 150 nm. The cellular space between the apical surface and the nucleus contains a large number of mitochondria. These are particularly abundant at the points of intensive branching of the ciliary rootlets. Narrow and dark oval nuclei 5-8 µm long and 2-4 µm wide are found in the expanded part of the cell body. The central processes of these cells find their way past the basement membrane.

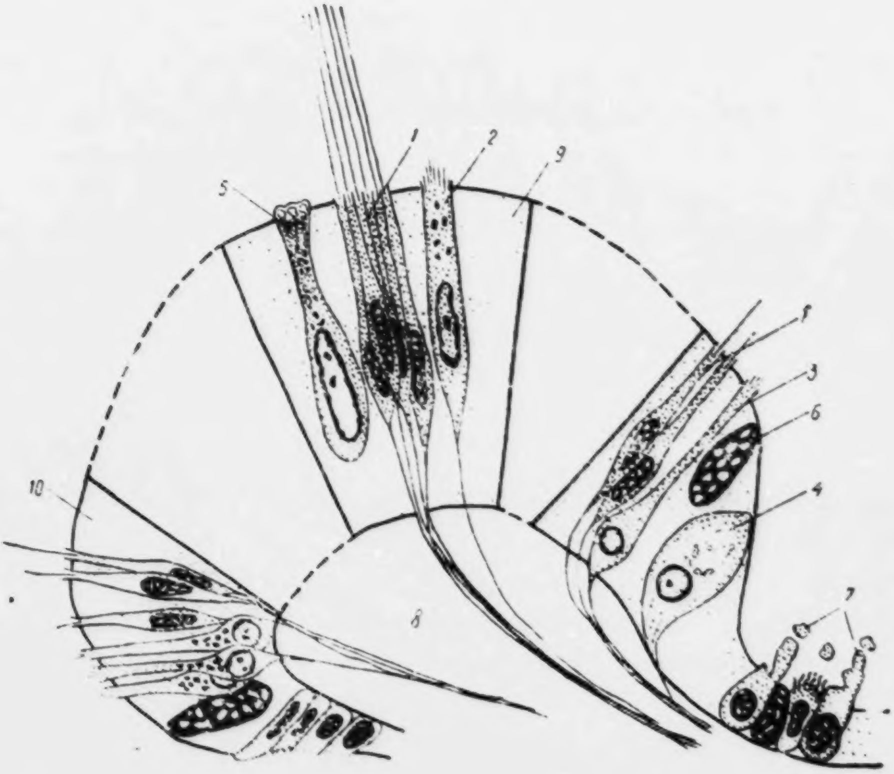


Fig. 22. Distribution of cells in the epithelium of the abdominal sense organ of the Yezo scallop. 1 - sensory cells of the first type with a single long cilium; 2, 3 - sensory cells of the second and third types with a bundle of short cilia; 4 - sensory cells of the fourth type found in the marginal region of the epithelium; 5 - secretory cells of the central zone; 6 - mucous cells; 7 - epithelial cells of the band of tissue; 8 - nerve fibres; 9 - central zone of epithelium; 10 - marginal zone of epithelium

Receptor cells of the second type are comparatively rare in the central zone of the organ (Fig. 22). They are about 20 μm long, with a diameter of10 μm in the widest part and 3-6 μm in the apical part. They have a spherical light-coloured nucleus with a diameter of 6-8 μm. The apical surface of the cell bears a bundle of short cilia. In individual sections, the cells of the second type appear to have a central process which penetrates through the basement membrane.

The relative number of cells of the first type decreases in the marginal zone of the abdominal sense organ. Here, we largely encounter cells of the third type, in many ways similar to the cells of the second type, but with a narrower and longer perinuclear part which ends in a bundle of short cilia (Fig. 22). Accumulations of dark granules of different sizes are seen above the nucleus. The expanded basal region of the cell passes into a narrow process which passes through the basement membrane.

In individual sections of the marginal zone, large receptor cells of the fourth type with a light-coloured layered cytoplasm, a light-coloured nucleus and a thick basal process are encountered right next to the base of the organ. In this part of the epithelium, mucous cells with light-coloured vesicles are often encountered (Fig. 22).

Other cells are encountered alongside the receptor cells in the central zone of the organ. They measure 26-32 μm in length and 6-7 μm in width. A large nucleus occupies a substantial part of the cell. Cilia and central processes are not observed in these cells. Granules of secretion are seen in some of the epithelial cells, which gives grounds for assuming that they perform a secretory function.

When examining the surface of the abdominal organ with a scanning electron microscope, we note the extremely high density of the cilia in the central part of the organ; they completely cover the surface of the epithelium. In the region of the marginal zone where the number of cells of the first type decreases, bundles of short cilia of the third type of cells are seen together with those of the first type (Fig. 23).

In Moir's studies of the abdominal sense organ of *P. magellanicus* (Moir, 1977b), only two types of cells were described, receptory and sensory. Structurally, these cells are identical to the first type of receptor cells and the secretory cells described in the Yezo scallop.

Behavioral experiments have shown that an intact scallop is highly sensitive to the vibration of the bottom, as well as the vibrations transmitted through the water. In these experiments, the scallop was placed on a special vibrational platform, or suspended 15 cm above it. When exposed to a vibration frequency of 100-600 Hz, the scallop responded by closing its valves, or by contracting the velum of the mantle and its tentacles. In a scallop with an amputated abdominal organ, the sensitivity threshold increased more than 100-fold. These experiments are direct proof that the abdominal sense organ is responsible for picking up vibrations in the water (Zhadan, Semenkov, 1982).

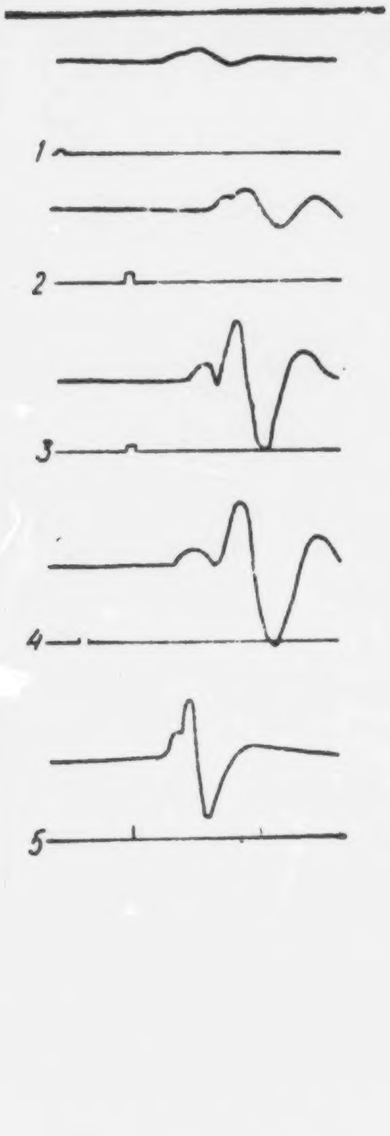


Fig. 24. Total impulse response registered in the right branch of the nerve during stimulation of the abdominal sense organ of the Yezo scallop with single mechanical impulses of various amplitude (1-4). Action potential in the right branch of the nerve of the abdominal sense organ (5). Amplitude of mechanical stimulus: 1 - 0,04 µm, 2 - 0.2 µm, 3 - 0.8 µm, 4 - 8 µm. Distance from abdominal organ to registering electrodes 8 mm for 1-3, and 16 mm for 4-16. Distance between the stimulating and discharge electrodes 8 mm for 5; time criterion 20 ms; potential 1 mV; temperature 12°C

Electrophysiological experiments were also performed on an isolated abdominal organ. The impulse activity was led off either from a whole nerve, or from thin bundles of nerve fibres consisting of 3-5 active units. The organ was stimulated by individual mechanical jolts or by vibration. When leading off from a whole branch of the abdominal nerve, the response to a light mechanical jolt was a short impulse discharge. When the amplitude of the stimulus was increased, the impulse frequency in the discharge gradually increased. A further increase in the intensity of the stimulus occurred as a result of the summation of individual impulses, and the response took the form of two-phase oscillation of the potential (Fig. 24). The amplitude of the total potential was directly related to the intensity of the mechanical jolt, since it reflected the instantaneous frequency of the impulses and the number of simultaneously stimulated nerve fibres.

In the right branch of the nerve of the abdominal sense organ, the response consisted of two components (Fig. 24). The first component of the response displayed a shorter latent time of initiation and a smaller amplitude as compared with the second one. When the leading off point of the impulse from the abdominal organ was eliminated, the latent time of initiation of both components increased because of a delay due to impulse transmission time. However, an increase in the difference between the initiation time of the first and second components of the response was observed at the same time. This indicates that the right branch of the nerve of the abdominal organ contains fibres differing in the rate of conduction; consequently, they differ in diameter. At the same time, the first component of the total response arises in the thick nerve fibres, while the second component arises in the thinner nerve fibres. When the rate of impulse conduction was measured by recording the total response at two points 3 cm from each other in the right branch of the nerve, we found that it was equal to 0.42 m/s for the first component of the response, and 0.32 m/s for the second component at 12°C.

Measurements similar to those described above were also carried out for the left branch of the nerve of the abdominal organ. A three-component response was recorded in this branch. The first component was equal to 0.9±0.1 m/s at 12°C, while the conduction rate of the second and third components coincided with the values derived for the right branch of the nerve. The difference in the rate of conduction along the afferent fibres indicates primarily that they innervate different types of mechanoreceptor cells. This assumption has been proven to some extent in experiments where the abdominal organ was removed. After removal of the organ, the left branch of the nerve retained only the first component of the response. This response arose when single mechanical jolts were applied in the region of the band of tissue. It can therefore be said that the fibres with the highest conduction rate innervate the mechanoreceptors of the band of tissue, while the rest of the fibres are connected to the mechanoreceptors of the abdominal organ. In the experiments with leads taken from the thin bundles of nerve fibres innervating the mechanoreceptors of the band of tissue, we found that the latter were functionally similar to the mechanoreceptors of the mantle margin. These mechanoreceptors reacted with a brief impulse discharge to a single jolt, and they quickly adapted to repeated mechanical stimuli and vibration. The thresholds to single mechanical jolts applied in the region of these receptors were equal to 0.8-2 μm.

Further analysis of the properties of the mechanoreceptor cells of the abdominal sense organ was carried out by leading off impulse activity from thin bundles of nerve fibres while stimulating the organ with vibration of different frequency. The experiments showed that the nerve of the abdominal sense organ consists of two groups of fibres which innervate mechanoreceptor cells with different functional properties.

The fibres of the first group are part of the overwhelming number of the analyzed bundles of nerve fibres. In these fibres, the impulse response registered when the organ was stimulated with vibration in the frequency range of 20 to 600-1000 Hz; the mechanoreceptors innervated by these fibres displayed maximum sensitivity to vibration in the frequency range of 200-300 Hz. The threshold of the impulse reaction gradually increased when the frequency of the stimulus was either decreased or increased.

In the fibres of the second group, the reaction to vibration registered in a narrower frequency range, from 20 to 350 Hz, with the minimum threshold in the frequency range of 100-150 Hz.

The electrophysiological data on the presence of two types of mechanoreceptors that differ in the type of dependency of the reaction threshold on vibration frequency are quite consistent with the results of the morphological studies in which two types of receptor cells were established in the sensory epithelium. It can be said that the more frequently encountered fibres of the first group innervate the numerous sensory cells of the first type with a single long cilium, while the less commonly encountered fibres of the second group belong to the comparatively scarce multiciliated receptor cells.

The reaction threshold greatly depended on the stimulation site. The mechanical stimulation was the most effective when the tip of the stimulator came in close contact with the base of the abdominal organ. In this case, the minimum reaction threshold registered in the fibres of the first group was equal to 0.006 µm at a frequency of 240 Hz, and in the fibres of the second group 0.008 µm at a frequency of 150 Hz. When the tip of the stimulator was applied to the ends of the cilia of the receptor cells, the reaction threshold of the abdominal organ increased 6—12-fold. A comparatively smaller change in the effectiveness of stimulation was observed when the tip of the stimulator was moved 2 mm from the tips of the cilia. In this case, the threshold increased 1.5—3-fold. It should be said that none of these methods of stimulation altered the frequency—threshold characteristics for the fibres of either group.

The above data on the absolute threshold values distinguish the abdominal sense organ from the other mechanoreceptors of the mollusks, and give grounds for regarding this structure as a specialized mechanoreceptory organ, the function of which is to sense vibrational signals. The theoretical possibility of weak vibrations being picked up by the organs of equilibrium (mechanoreceptors of statocysts) of nudibranchs and gastropods has been demonstrated in electrophysiological experiments. However, the threshold values of vibration that caused an impulse reaction in these experiments were higher than those derived for the abdominal organ by more than two orders of magnitude. It should also be said that the statocysts are organs of equilibrium, and the sensing of vibration by them is probably related to the nonspecific reaction of the hair cells of this organ to mechanical stimulation.

The data on the high sensitivity of the abdominal organ to vibration permits us to advance a hypothesis on the biological role of this organ. A comparison of the habitats and the structural characteristics of the body in bivalves with an abdominal sense organ shows that this structure is found only in those bivalves which do not have developed siphons, i.e. in those relatively accessible to predators, since they live either on the surface of a substrate or slightly beneath its surface. The high sensitivity of the abdominal organ to vibration is in this connection an important evolutionary acquisition which provides the animal with information on an approaching predator. It is possible that, because of its sensitivity to mechanical stimuli, the abdominal organ can also serve as a means for registering the rate of water flow in the mantle cavity, and in this way contribute to the regulation of the feeding and respiration rate of the animal. This deduction appears to be quite conclusive, since the organ is located on the route of the main flow of water through the mantle cavity.

6. FEEDING AND DIGESTIVE ORGANS

6.1. Feeding organs

As in other bivalve mollusks, the feeding organs in the Yezo scallop consist of the gills and the oral lobes; borderng on the latter is a labial apparatus characteristic of the Pectinidae and Limidae. In Jorgensen's opinion (Jorgensen, 1966), the mantle with the pallial tentacles should also be included among the feeding organs in bivalve mollusks. The mantle margins form the suction aperture through which the water current with suspended particles passes. In this zone of first contact with the water, the sensory function of the mantle margin is particularly important. By preventing coarse particles from getting into the mantle cavity, the pallial tentacles act as filters, and so they are developed to the greatest extent in the animals living on substrates with a moderate and a high content of water-suspended particles. A high degree of development of the tentacles in the Yezo scallop indicates that they contribute to the primary sorting of the particles.

There are several theories regarding the feeding of filtering mollusks (see Bayne et al., 1976; Jorgensen, 1966; Owen, 1966; Purchon, 1977). The most widespread is the theory of particle sorting according to particle size and mass. The "mucous trap" theory is the less widespread one; according to this theory, the sorting of food particles in bivalves is carried out mainly by the mucous layer covering the gills. The mucus is secreted by the glands of the frontal surfaces of the gill filaments and, to some extent, the base of the gills. The mucous "fabric" serves as a sieve which catches the particles as they pass through the gill filaments; the beating of the frontal cilia transports it to the ventral margin of the gills where it is twisted into mucous strings directed through the oral lobes into the mouth and then into the stomach; the unsuitable particles sorted out by the lobes are returned to the rejection tracts of the mantle. However, the "mucous trap" theory is questioned by a large number of researchers. They consider it unlikely that a highly developed filtering branchial apparatus would not contribute to the feeding process (cit. Bayne et al., 1976). The sorting of particles in the gills is apparently ensured by the combined action of the filtering apparatus, the mucous "fabric" and the muscular activity of this organ (Owen, 1966).

The functions of the oral lobes are similar in all the filtering bivalve mollusks (see Jorgensen, 1966; Owen, 1966; Purchon, 1977).

The material collected and initially sorted on the gills is transported from their marginal grooves to the surface of the oral lobes. In bivalve mollusks, the transfer of material from the gills to the oral lobes takes place only when each of the oral lobes comes into contact with the margin of the demibranch (cit. Bayne et al., 1976). On the surface of the oral lobes, there is an intricate system of ciliary tracts formed by ridges and grooves. Despite the high degree of variability of their distribution in different species of mollusks, the three main tracts are the receiving tract, the rejection tract and the particle resorting tract (Owen, 1966). The cilia on the tops of the ridges beat in the direction of the mouth, and represent the main tract of particle reception; the cilia on the bottom of the grooves between the ridges beat in the direction of the free margin of the lobes, along which the main tract of particle rejection passes; the resorting tracts located on the lateral surfaces of the ridges can return the material either to the receiving tracts, or to the rejection tracts. In addition to the main tracts, a system of countercurrents was found on the entire surface of the ridges and grooves. As a result of the overall action of the sorting system of the oral lobes, only the most insignificant part of the material supplied to the surface reaches the mouth. The bulk of the material is rejected from the free margins of the lobes and enters the rejection tracts of the mantle, after which it is excreted as pseudofeces. We do not know whether the oral lobes participate directly in the sorting of food particles from the water surrounding them, as demonstrated for the larvae of oysters (Jorgensen, 1966).

Several investigations have been devoted to the study of the structure and functional morphology of the oral lobes and labia in the Pectinidae (Dakin, 1908; Yonge, 1953; Gilmour, 1964; Bernard, 1971). However, the literature contains no description of the histological structure of these organs in the scallop. Only Dakin's brief data for *P. maximus* are available (Dakin, 1908). Our histological study of the oral lobes and labial apparatus in the Yezo scallop has revealed a number of characteristics which are probably common to other members of this order.

6.1.1. Oral lobes

The two pairs of oral lobes in the Yezo scallop are found in the anterior part of the body between the ends of the gills and the mouth, with an inner and an outer lobe on each side (Fig. 25). The lobes consist of thin light-coloured triangular—oval lamellae which are attached by their broad bases to the digestive gland and partly to the gonad, gills and mantle; their straight sides concresce with the labial margins up to midpoint, and the opposite sides are free. The surfaces of the lobes directly facing the mouth are plicate, the rest are smooth. The rugosity is formed by deep grooves and ridges, the tops of which are always directed towards the mouth. On each lobe, there are about 16-17 ridges, 3-4 of the anterior ones being much larger than the plicae of the posterior part of the lobes. The larger anterior ridges apparently prevent coarse and unwanted particles from getting into the mouth. At the point where the plicate surfaces of the two lobes come together, an oral groove leading to the corner of the mouth forms on each side.

The oral lobe consists of a layer of loose connective tissue covered with one-layer prismatic epithelium resting on the basement lamina. The connective tissue contains groups or individual small free spherical cells with 1-2 nuclei surrounded by a more or less wide rim of cytoplasm; spindle-shaped cells are less common. The vesicular elements described in the connective tissue of other species of bivalves are not found in the Yezo scallop. The connective-tissue stroma of the lobes is pierced by numerous solitary muscle fibres and a hemal reticulum. Bundles of longitudinal muscle fibres lie directly under the epithelium.

The smooth side of the oral lobes is covered with cubical epithelium consisting of border, mucous and ciliated cells. The border elements have a small brush border, an oxyphilic, mildly PAS-positive cytoplasm and a large spherical nucleus. We occasionally encounter cells with hypertrophied, possibly polyploid nuclei and a very large nucleolus. The numerous mucous cells are spherical; their nuclei are often pycnotic, and are found at the basal boundary of the layer. The basal portion of the cytoplasm probably contains promucin and protein. The apical, coarsely-vesicular part of the cytoplasm reacts strongly to Schiff's reagent, and far less intensely to Heidenhain's azan stain and alcian blue. Cells of this type apparently produce a mixed type of mucus which contains glycoproteins and to a smaller extent glycosamineoglycans. The secretion of the less commonly encountered and smaller spindle-shaped mucous cells contains only glycosaminoglycans. Ciliated cells on the smooth surface of the lobes are comparatively rare in the scallop. The majority of them have a well-developed ciliary apparatus, oval nuclei and an oxyphilic cytoplasm. These cells apparently participate in the transport of particles, directing them to the rejection tracts on the plicate surfaces of the oral lobes. Cells with a single flagellum, probably sensory cells, are also rarely encountered in the epithelial layer. The presence of receptor cells on the smooth surface of the lobes was noted in *Pecten maximus* by Dakin (Dakin, 1908).

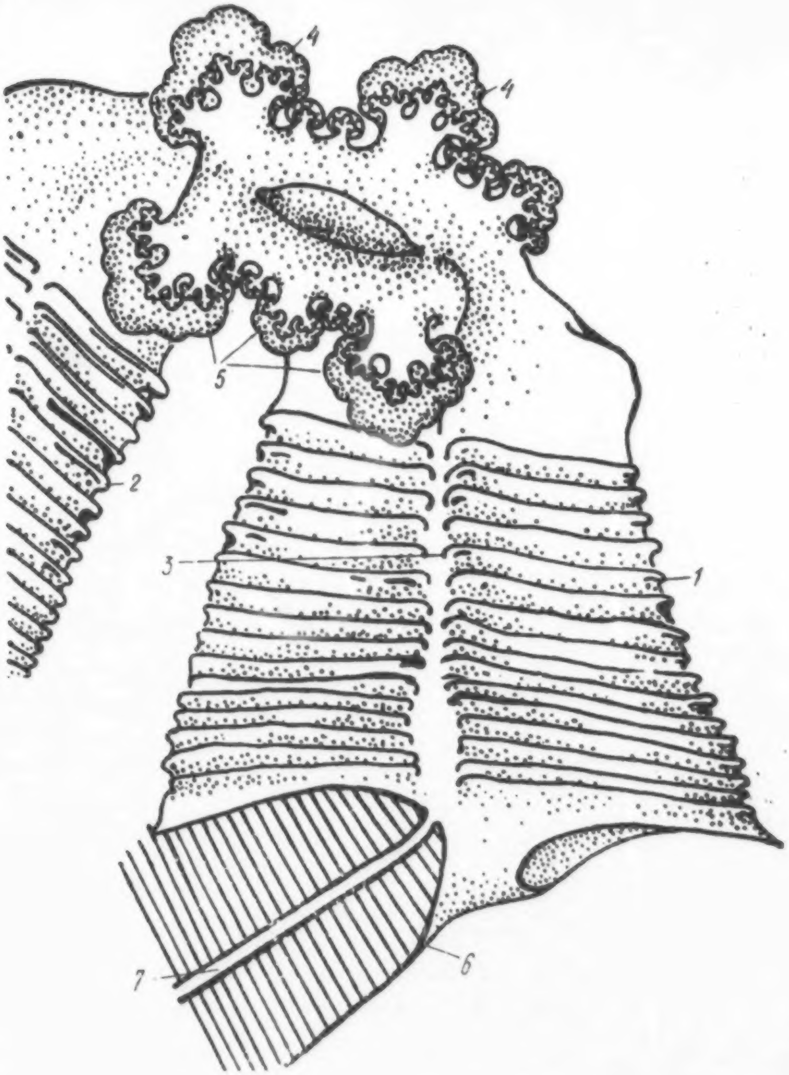


Fig. 25. Diagram of oral lobes and labial apparatus in the Yezo scallop. 1, 2 - plicate surfaces of outer and inner lobes with glandular area; 3 - oral groove with lateral and proximal areas; 4 - upper lip with two hypertrophied lobes; 5 - lower lip with three lobes; 6 - distal ends of outer gill; 7 - oral groove of gill

The rugose surface of the oral lobes is formed by a group of grooves and ridges. The well-developed ridge consists of an apex with a secondary furrow and two slopes, an anterior gently sloping one directed toward the mouth, and a posterior steep one. The epithelium covering them differs in the height of the cells and the degree of development of the ciliary apparatus. The entire surface of the ridges and grooves has a finer secondary rugosity, probably matching the pathways carrying particles in the direction opposite to the main tracts of particle reception, rejection and resorting. The presence of a system of countercurrents in addition to the well-developed main system of ridges and grooves points to a highly active sorting function in the oral lobes of the Yezo scallop.

The epithelium of the plicate surface of the oral lobes (one-rowed, pseudostratified, tall prismatic, ciliated) consists of ciliated and mucous cells. Three varieties of ciliated epitheliocytes can be distinguished, i.e. ciliated non-secretory, ciliated secretory and smaller narrow-prismatic cells. Cells of the first variety line the bottom of the grooves. They have a cylindrical shape, oxyphilic cytoplasm, and an oval-elongated nucleus with coarse chromatin bodies. The ciliated-secretory elements form the base of the epithelium of the apices and slopes of the ridges. These conical or cylindrical cells with a more or less developed ciliary apparatus produce an oxyphilic secretion which reacts negatively to protein and acidic mucus. It is quite probable that these two varieties of ciliated cells (with secretion and without it) correspond to a different functional state of the same epitheliocytes. The narrow-prismatic cells are comparatively rare; they are distinguished by a small elongated hyperchromatic nucleus. The nature of these cells is still unknown.

Two types of specialized mucous elements are encountered in the epithelium of the plicate surfaces of the oral lobes. Mucocytes of the first type are found in the epithelium of the ridges, predominantly at the apex and especially near its groove. They are highly prismatic or flask-shaped. Their cytoplasm is polychromatophilic in the basal zone, and stains for mucus in the central and apical zones. The nuclei of mucocytes, spherical with a very light-coloured karyoplasm and a large nucleolus, are found at the basal boundary of the layer; hyperchromatic pycnotic nuclei are often encountered in mature cells. Mucocytes of the second type, found in the epithelium of the grooves, are cup-shaped or flask-shaped; their cytoplasm is not basophilic, but reacts positively to alcian blue or Schiff's reagent, as well as to protein. These two types of mucocytes apparently produce a different type of mucus; the mucocytes at the apex of the ridges produce a mucus consisting of a mixture of glycosaminoglycans and glycoproteins, whereas the mucocytes of the grooves secrete either glycosaminoglycans, or neutral mucoproteins. These two varieties of mucous secretion are bound to differ in viscosity as well, which is of great significance during the formation of both pseudofeces and the food bolus.

The plicate surface of the lobes passes into a small smooth area directly at the mouth (Fig. 25). The highly prismatic epithelium lining it consists of three main types of cells. The ciliated secretory elements and mucocytes are similar to those in the epithelium of the ridges of the lobes. The third type of cells (glandular) is highly unique; it is not encountered in any of the other parts of the digestive tract. These are large flask-shaped cells. Their fibrillary cytoplasm is basophilic, and reacts strongly to PAS-positive substances and to protein. Vesicles with an acidic mucus are sometimes detected in the apical or central part of the cells. The nuclei of these glandular cells are large, transparent, and almost spherical.

These features characterize the basophilic glandular elements as high specialized ones which produce a secretion with a distinct protein component. As we have already noted, these cells are specific for the epithelium of the smooth circumoral region of the lobes, where, closely spaced, they form an extensive glandular area which unquestionably plays and important functional role. Perhaps the protein-enriched mucus produced here is highly viscous, which would contribute to the formation of mucous food strings or lumps to be transported to the mouth. On the other hand, we must not exclude the possibility that the secretion produced here is of a protein nature, and is responsible for the initial enzymic processing of food particles. This role is usually attributed to the secretion of specialized salivary gland. There is no separate salivary gland in the Yezo scallop. It is quite probable that the described circumoral glandular area is its functional analogue.

6.1.2. Labial apparatus

As in other Pectinidae, the labia in the Yezo scallop consist of the labia proper and their elongated hypertrophied processes. The latter, in the form of racemose structures, surround the mouth and the proximal oral grooves of the lobes. The labial processes can easily expand when relaxed, or contract abruptly, closing the mouth completely. The labia proper, which form the oral aperture, consist of a thick layer of loose connective tissue abounding in blood vessels and longitudinal muscle fibres, and a thin layer of ciliated prismatic epithelium. The upper lip consists of two large hypertrophied lobes, the lower one consists of three (Fig. 28). Between these main lobes, the free margins of the labia bear much smaller lobules. A characteristic feature is the treelike branching of the lobes and lobules into even smaller papillae, a structural unit of the labial apparatus. The ends of the labial palps are continuous with the oral lobes (Fig. 25), and a great similarity is noted in their histological structure; Dakin noted the same for *P. maximus* (Dakin, 1908).

A papilla consists of a pedicle and a head. The papillary pedicles on the whole make up the smooth part of the labial apparatus, while the head makes up the pectinate part. The pedicle of a papilla is lined with cubical epithelium consisting of cuticular and mucous cells. The cuticular cells have a brush border containing glycoproteins, a large nucleus, large vacuoles in their cytoplasm, PAS-positive granules, and less commonly vesicles of an indistinct form; in some cases, the latter resemble the vesicles of the ciliated secretory cells of the lobes. The mucus cells are abundant, large, oval—cup-shaped, and they contain glycosaminoglycans and/or glycoproteins. Ciliated cells are not found here.

The head of a papilla is pectinate, and consists of a fibrous connective-tissue base with well-developed muscle fibres. The overlying prismatic ciliated epithelium with a 1—2-rowed arrangement of the nuclei forms ridges and grooves. It consists of ciliated, ciliated-secretory and mucous cells similar to those of the epithelium of the oral lobes. However, the morphological similarity of the ciliated and ciliated secretory elements is more manifest in the labial apparatus; perhaps the first are capable of transforming into the second ones, being their immediate predecessor. Mitoses are observed exclusively in the ciliated cells.

The course of the ciliary pathways that direct the flow of particles in the labial apparatus of *P. maximus* has been examined in detail by Gilmour (Gilmour, 1964). A similar mechanism of transport apparently exists in the Yezo scallop as well. At the same time, an important role is played by the active secretion of mucus on the pectinate surface of the labial papillae. The material that gets onto the outer surface of the upper lip passes into the rejection tracts of the oral lobes; from the outer surface of the lower lips, the material passes into the rejection tracts of the foot. In Gilmour's opinion, the highly developed labial apparatus of the scallop should be regarded as an adaptation for protecting the food string against water action, the latter being stronger in pectinids because of the reduction of the anterior end of the body and a smaller mantle cavity. The food string in the scallop also has to be protected against the water currents arising from the abrupt closing of its valves (Dakin, 1908). It is believed that the function of the hypertrophied labia in pectinids underwent specialization not so much for the retention of food particles, as for the sorting of them (Bernard, 1971).

6.2. Digestive organs

The digestive system in the Yezo scallop consists of an oesophagus, a stomach, a digestive gland, and an intestine (fore-intestine, recurrent intestine and rectum) (Fig. 26). Because of the reduction of the head region of the body, there is no oral cavity, pharynx, or the radula and salivary glands associated with it . This has resulted in a more developed posteroventral region with a longer intestine and a shorter oesophagus (Graham, 1949) (Fig. 26). According to Graham, the stomach did not conform to the general evolutionary course of the pectinids; its development was not affected much by the size of the other parts of the body. As a result, the stomach of the scallop retained the same proportions as the most primitively formed bivalve stomachs.

Digestion in the Yezo scallop is both extracellular in the stomach, and intracellular in the terminal regions of the digestive gland. Intracellular digestion is much more prevalent; therefore, the digestive gland is more developed than the rest of the digestive organs. Because of the external similarity between the digestive gland of mollusks and the liver of vertebrates, as well as its content of glycogen and the secretory activity of the cells of the digestive ducts, the terms liver or hepatopancreas are used extensively, which is incorrect. The digestive gland, or diverticulum, of the mollusk is not the same as the liver of vertebrates, as it is the central organ of intracellular digestion (see Leibson, Usheva, 1979). According to the literature, the process of digestion in the Yezo scallop has not been researched, but, on the whole, it is probably similar to that described by Reid for *Lima hians* (Reid, 1965, 1968). On the basis of the literature and our own data, the digestive system in the Yezo scallop can be pictured in the following way.

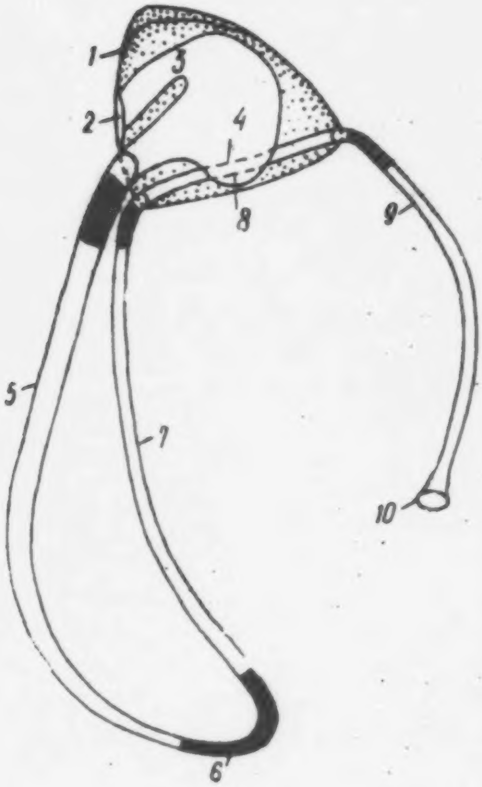


Fig. 26. Organs of the digestive tract. 1 - digestive gland; 2 - oesophagus; 3 - entry of oesophagus into stomach; 4 - stomach; 5 - fore-intestine; 6 - transition of fore-intestine into recurrent one; 7, 8 - recurrent intestine; 9 - rectum; 10 - anus. Analyzed parts of intestine blackened.

The mucus-covered material collected and sorted by the gills, oral lobes and labial apparatus passes into the oesophagus. The main function of the latter lies in the conveyance of the food particles and additional processing of them with mucus. The Yezo scallop does not have any special oesophageal glands, but as we shall show later on, distinctive glandular mucus grooves form in the "corners" of the oesophagus. The material goes into the stomach in the form of a mucous string, and is sent by the strong beating of the ciliated lining of the anterior part of the stomach into the dorsal hood and farther into its cecal end, into which the tip of the crystalline style is lowered in the Yezo scallop. The crystalline style is a hyaline rod consisting of glycoproteins and amylolytic enzymes. The main part of the style is found in the fore-intestine, and, under the effect of the ciliary movements of the intestinal lining, it rotates so that the mucous strings with food particles gradually wind onto the head of the style and move from the dorsal hood into the zone of the gastric shield. In the stomachs of freshly opened Yezo scallops, one can find a mass of mucous food material wound onto the head of the crystalline style. With low pH values of the gastric fluid and under the effect of the mechanical friction of the rotating style against the surface of the gastric shield covered with cuticle, the mucous food mass and the style substance dissolve into component parts. The gastric juice acidifies mainly because of the products of the final stages of digestion, which enter the stomach from the digestive gland. As a result of this, the viscosity of the mucus in the stomach decreases, which also contributes to the disaggregation of the mucous food mass. The resulting particles mix with the enzymes of the style, and in the case of the Yezo scallop possibly with the enzymes secreted by the protein cells of the stomach lining, and fall into the general circulatory flow of gastric fluid, created by the cilia of the fundus and the walls of the stomach. The circulatory flow directs the particles from the left part of the stomach into the right part where the sorting system of the stomach and the majority of digestive ducts are located. The small, but heavy particles get into the grooves of the folds in the sorting zone, and are removed from the stomach through the intestinal groove of the fore-gut. Large, but light particles, or masses of them are redirected by recirculation currents into the dorsal hood and to the head of the style for further reduction. The finest particles from the suspension of gastric juice, which are suitable for digestion and have already been exposed to the action of enzymes in the stomach, are directed in the form of colloidal material to the duct openings of the digestive gland.

The ducts of the gland consist of two grooves, a ciliated and a non-ciliated one. The ciliated groove creates a circulatory current which flows from the gland into the stomach; in the non-ciliated groove, the hydraulic difference in pressures creates a countercurrent which sucks in the food material from the stomach and directs it into the digestive ducts. The digestive cells of the ducts absorb the food material by endocytosis. The food material undergoes intracellular digestion in the digestive vacuoles. In the three groups of bivalve mollusks of the order Gastrotetarctica, the digestion of proteins and lipids is intracellular, whereas polysaccharides are digested in the stomach (Reid, 1968). The undigested food remains are returned to the sorting zone of the stomach from the gland, and then to the intestine where feces are formed. This is achieved by secretion of mucus into the intestinal lumen and pH changes of the stomach contents, which increases the viscosity of the mucus and results in the solidification of the feces. The feces retain their form for a comparatively long time after excretion from the intestine; this prevents them from getting into the mantle cavity of the animals.

It is believed that absorption and digestion do not take place in the intestine (Purchon, 1977). This opinion will probably be reviewed in connection with the discovery of hydrolases such as esterase, arylomidase and acidic and alkaline phosphatase in the intestine of bivalve mollusks, specifically in *L. hians* which is closely related to the scallops (Reid, 1968). However, we still do not have enough evidence that the intestinal epithelium in the Yezo scallop participates in the processes of absorption and digestion.

6.2.1. Oesophagus

The oesophagus is an anteroposteriorly flattened tube embedded in the tissue of the digestive gland. Grooves are seen in the corners of the oesophagus; they are the continuation of the grooves of the oral lobes. The oesophageal wall is composed of one-layer epithelium, subjacent loose connective tissue and a layer of circular smooth muscle fibres (Fig. 27); in addition, large bundles of longitudinal muscle fibres extend from the oesophagus into the digestive gland. Perhaps the oesophageal wall of the Yezo scallop is capable of slight peristaltic movements which facilitate the transport of food into the stomach.

The epithelium lining the oesophagus is one-layered, multi-rowed, ciliated, and high prismatic (low prismatic in the corners of the oesophagus). The thickness of the epithelial layer in 2—3-year-old scallops varies from 150-400 µm on the apices of the folds to 50-150 µm in the spaces between them. The epithelium rests on the basement membrane with the subjacent connective-tissue layer. The basement membrane forms numerous evaginations in the epithelium.

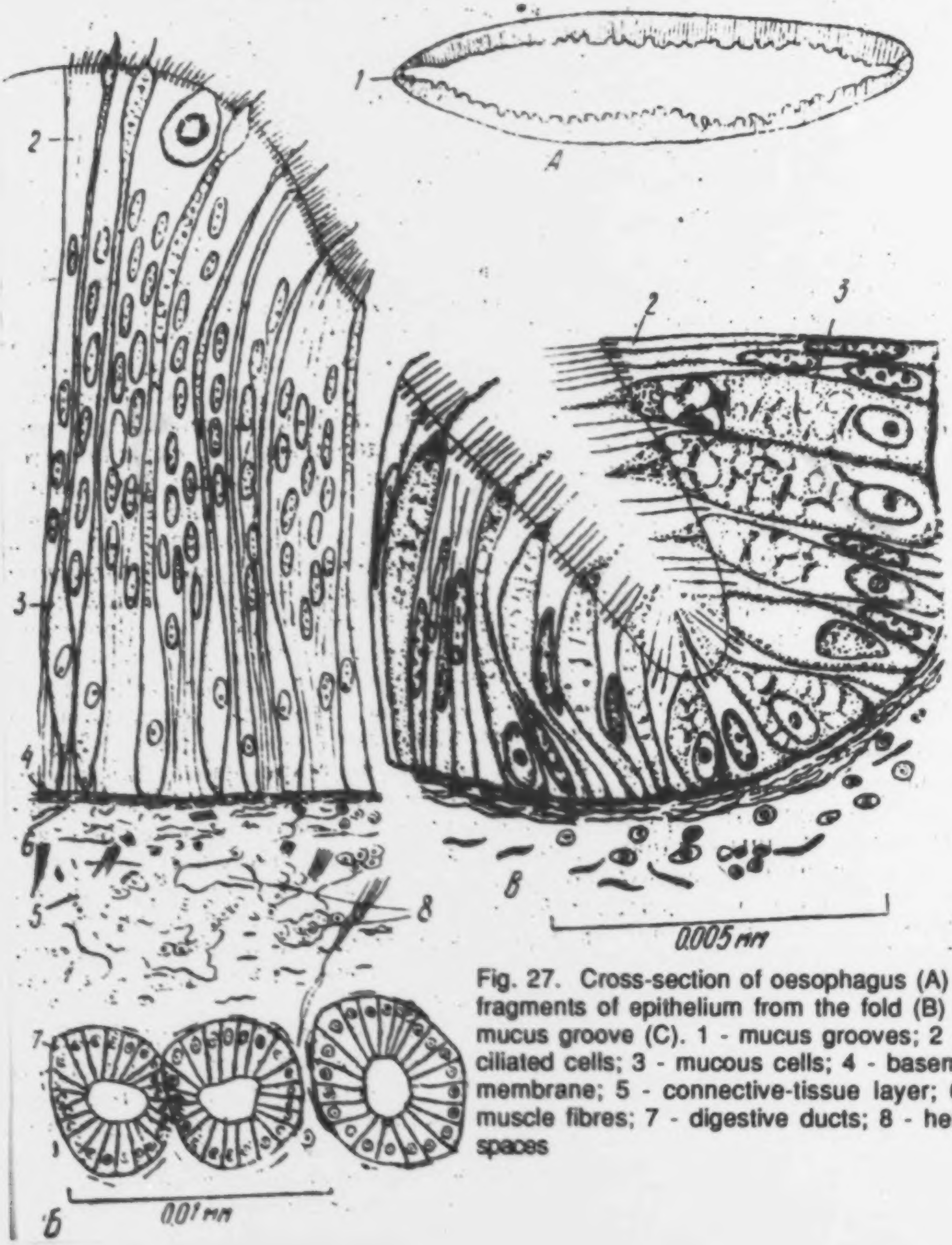


Fig. 27. Cross-section of oesophagus (A) with fragments of epithelium from the fold (B) and mucus groove (C). 1 - mucus grooves; 2 - ciliated cells; 3 - mucous cells; 4 - basement membrane; 5 - connective-tissue layer; 6 - muscle fibres; 7 - digestive ducts; 8 - hemal spaces

Cristate longitudinal folds formed by high epithelial cells are clearly observed on the surface of the oesophagus. The rugosity increases near the point where the oesophagus passes into the stomach, and it is more manifest in older individuals. In a scallop that has just been opened, an irregular transverse rugosity is also observed in the oesophagus.

The cellular composition of the oesophageal epithelium differs somewhat from that of the lobes and labial apparatus. For example, ciliated secretory elements were not found in the oesophageal epithelium, and cells with a small hyperchromatic nucleus were rarely encountered. The ciliated elements are extremely high and thin (especially in old individuals), and are characterized by a well-developed ciliary apparatus. Their nuclei are oval-elongated, with distinct boundaries, and with 1-2 small nucleoli in the central and apical zones of the epithelial layer. The apical expanded parts of the ciliated cells bear an oxyphilic brush border rich in proteins and poor in polysaccharides. The granular or vesicular cytoplasm is basophilic near the nucleus, where it displays a distinct reaction to the total proteins. In the part where the oesophagus passes into the stomach, the ciliated epitheliocytes were seen to form bulb-shaped evaginations, and to discharge from them large vesicles with granular contents by means of clasmatosis; the nature of the secretion is still unknown.

As in the epithelium of the lobes and labial apparatus, the unicellular glandular elements in the oesophageal epithelium of the Yezo scallop are exclusively intraepithelial. The mucocytes are predominantly localized in the "corners" of the oesophagus, where they form continuous glandular areas; strictly ciliated cells are clearly less abundant here. The mucocytes of these zones are usually larger and more brightly pigmented than on the sides of the oesophagus; their number decreases in the direction of the stomach. The mucous cells are characterized by a flask-shaped or conical (less commonly cup-shaped) form and a small bulb-shaped expansion at the apical end which projects into the lumen of the oesophagus. Their secretion, lumpy or vesicular-frothy reacts strongly to mucus with Heidenhain's azan stain and alcian blue, moderately to polysaccharides, and very weakly or not at all to proteins. With toluidine blue (pH 3.8 and 6.0), the secretion of mucocytes produces an intense metachromatic reaction which intensifies sharply after sulphatization; at the same time, the number of metachromatic cells increases significantly. These results permit us to conclude that the secretion of oesophageal mucocytes in the scallop is a compound of sulphatized and nonsulphatized glucosoaminoglycans and glycoproteins. The nuclei of most of the oesophageal mucocytes are located in the central, nuclear, zone of the layer; optically, they are similar to the nuclei of ciliated cells. We also observe secretory elements, the nuclei of which occupy a basal position in the layer; these are large, round and hypochromatic cells with a hypertrophied nucleolus, similar to the nuclei of the mucocytes of the oral lobes.

The histogenetic interrelations between the ciliated and mucous elements of the oesophagus are still unknown. The discovery of ^{3}H-thymidine-labelled nuclei in the ciliated cells permits us to assume that they are transformed into mucocytes, which does not exclude the possibility that they themselves are a source of mucocyte renewal.

One of the most remarkable characteristics of the oesophaeal epithelium of the Yezo scallop is the presence of a multitude of very large globular structures containing accumulations of rod-shaped or oval bacteria which apparently multiply within the epithelial layer. It is interesting to note that neither destructive changes, nor an increased number of phagocytes were observed in the adjacent parts of the epithelium. It is possible that symbiosis of the bacteria and epitheliocytes occurred in the case described by us. A multitude of similar structures was also found in the epithelium of the oral lobes, the labial apparatus, and in the epidermis of the scallop.

6.2.2. Stomach

The literature does not contain any data on the structure and functions of the stomach of the Yezo scallop, but the anatomy of the stomach of other species of pectinids has been researched quite thoroughly (Dakin, 1908; Graham, 1949; Purchon, 1957; Dinamani, 1967). The internal structure of the pectinid stomach has been described by Graham (Graham, 1949). Based on the form of the large typhlosole and the number of ducts opening into the stomach, Purchon (Purchon, 1957) assigned the scallop to the subclass Polisyringia of the order Gastrotetarctica, i.e. to the mollusks in which the digestive gland opens into the stomach by way of a large number of ducts connected in four large pits in its fundus, and the large typhlosole does not go into the sorting zone of the stomach.

All the researchers have noted the great structural similarity between the stomach in *P. maximus, Chlamys opercularis* and *P. crassicostatus* , and that of the similar species *L. hians* and *L. fragilis.* The stomach of the Yezo scallop is organized in a similar manner, though certain specific characteristics are also observed. These include an extremely developed dorsal hood with two longitudinal folds in it, a slight rugosity of the posterior sorting zone, greater reduction of the sorting chamber (cecum) in comparison with other scallops, and the absence of a sorting system in this cecum. We have used Graham's, Purchon's and Reid's nomenclature to describe the anatomy of the stomach (Graham, 1949; Purchon, 1957; Reid, 1965).

The stomach of the Yezo scallop is a small sacciform organ with a multitude of bends, recesses and folds in the mucous membrane, which perform a specific function. It is surrounded on the outside by tissue of the digestive gland. The oesophagus opens on the anterodorsal side of the stomach. At the point where the oesophagus falls into the stomach, there is a thickened circular fold of the mucous membrane with a well-developed muscular layer. A small groove extends at its base. The opening of the gastral fore-intestine is located on the posterior ventral wall of the stomach. The distance between the opening of the oesophagus and the fore-intestine is of diagnostic importance in the classification of bivalve stomachs. In the scallop, the anteroposterior diameter of the stomach is much smaller than the diameter between the lateral walls. Six basic structural units can be distinguished in the stomach of the Yezo scallop, namely the gastric shield, the sorting chamber with duct openings of the digestive gland, the dorsal hood, the large and the small typhlosole, the intestinal groove, and the left sacculation. The crystalline style enters the stomach from the opening of the mid-intestine; it rests on the gastric shield and descends into the cecal end of the dorsal hood. The gastric shield and the sorting chamber have a characteristic structure by which they are easily identified.

The gastric shield is a spherical plateau of the mucous membrane of the stomach floor. It is located on the left half of the stomach between the openings of the dorsal hood, the left sacculation and the fore-intestine. The gastric shield is covered with cuticle from above. The bulk of this cuticle is composed of a transparent hyaline lamella which can be removed from the underlying epithelium with comparative ease. The marginal parts of the lamella are very thin, and fused with the epithelium of the shield. The lamella abruptly thickens anteriorly, and forms a "tooth", the notch of which sits tightly on a small ridge of the mucous membrane of the stomach, found between the openings of the dorsal hood and the left sac. The lower margins of the tooth descend into the openings of these structures. At the base of the gastric shield in *L. hians* , Reid discovered a developed sorting system (Reid, 1965). No such system was found in the Yezo scallop, or in other scallops (Graham, 1949; Purchon, 1957; Dinamani, 1967). However, there is a small groove at the base of the right margin of the shield, and three short and large nonciliated folds separate its left margin from the posterior sorting zone.

The sorting cecum, a cecal process of the stomach wall, is considered to be the main sorting chamber of the stomach in bivalve mollusks. The cecum is particularly well-developed in the mollusks from the order Gastrotriteia. Graham has shown that the sorting cecum is significantly reduced in the scallop (Graham, 1949). Reid also believes that the sorting cecum in the mollusks of this order is simply a recess or canal between the openings of the oesophagus and the dorsal hood (Reid, 1965). The sorting cecum in the Yezo scallop is reduced to an even greater extent than in *P. maximus* (Graham, 1949; Purchon, 1957) and *P. crassicostatus* (Dinamani, 1967). It occupies an anterodorsal position between the openings of the oesophagus and the dorsal hood, and consists of a small recess in the base of the left fold of the latter. No sorting system was found on its bottom. Since the right duct lies right next to the reduced cecum, its sorting system probably replaces the one of the cecum.

The sorting zone is the functional analogue of the sorting cecum in the Yezo scallop. It is found on the bottom of the stomach. Its central part is plicate, and is easily identified during dissection due to the distinct fan-shaped arrangement of the longitudinal fold. The grooves of the latter converge at the posterior wall of the stomach in a single large intestinal groove which then passes into the fore-intestine. To the right of the plicate sorting zone, there is a smooth part which is usually called the posterior sorting zone in other mollusks. This is regarded as the extension of the sorting system of the right ducts (Reid, 1965). As a rule, this zone is also plicate in all of the scallops studied; however, only very fine, irregular and sparsely distributed folds are seen on its surface in the Yezo scallop. A small intestinal groove is found in the centre of the posterior sorting zone. The histological structure of the posterior sorting zone is very similar to that of the plicate part.

In the Yezo scallop, the ducts of the digestive gland open through the wall of the stomach. Approximately 30 of the ducts are combined in four groups with a common terminal opening on the bottom of the small oval recesses of the stomach, three of which are found on its right side, and one on its left side. Of the three right ducts, two are enclosed from the right part of the dorsal hood of the stomach by a thickening of the stomach wall which forms a distinctive overhang above them; the third, right duct is located near the oesophagus, beside the sorting cecum, i.e. at the boundary of the right and left sides of the stomach. A similar picture of duct distribution is shown for *L. hians* (Reid, 1965). Most of these stomach recesses with ducts have well-defined folds similar to or slightly thinner than in the sorting zone, and comprising the sorting system of the recesses themselves. Nonciliated tracts surrounded by small typhlosoles are also quite perceptible here. The tracts of the two extreme right ducts pass into each other, whereas the same tracts in the rest of the recesses are autonomous. Duct openings of the digestive gland are found on both sides of the nonciliated tracts.

The dorsal hood of the stomach in the Yezo scallop is exceptionally well-developed. It arises anterodorsally to the right of the oesophageal opening, then turns to the left, and extends in the anteroposterior direction, going deeper under the wall of the gastric shield where it ends blindly. Two well-developed folds, a right and a left one, stand out in the dorsal hood. One fold appears on the right, close to the opening of the oesophagus, passes along the centre of the hood, and disappears in the cecal end of it. Cristate processes, short transverse folds with "packets" of retiform finely plicate epithelium between them, extend from the fold to the bottom of the hood. They are much larger in the right part of the hood, than in the left. The other fold is much shorter and thicker, appears above the opening of the oesophagus, and is located mainly in the left part of the dorsal hood. It separates the dorsal hood from the reduced cecum. The posterior end of the left fold splits in such a way that one end of it disappears at the apex of the hood, and the other near the left sacculation. One ciliated groove is found on each side at the base of the lefthand fold. The large size and well-developed contour of the dorsal hood in the Yezo scallop indicates that it is the main food-receiving chamber of the stomach.

It should be said that the degree of development of the large typhlosole in the stomach is one of the main characters used for the classification of bivalve stomachs. As in the other scallops studied, the large typhlosole in the Yezo scallop does not form a lingula that projects into the sorting cecum. The lingula consists of an indistinct crest which extends from the apex of the large typhlosole of the fore-intestine into the left sacculation. The structure of the lingular wall is similar to that of the folds of the sorting system. Between the crest of the large typhlosole and the marginal part of the gastric shield, there is an extension of the large typhlosole in the form of a wide flat band. At the base of the crest of the large typholosole, there is an intestinal groove in which the grooves from the left sacculation converge with those of the adjacent right recess of the duct-bearing stomach wall. As in other scallops, the small typhlosole in the Yezo scallop is undeveloped and forms a well-defined ridge above the opening of the fore-intestine.

The left sacculation is located in front of the large typhlosole between the sorting zone and the dorsal hood in the left part of the stomach. As in the other scallops, the left sacculation in the Yezo scallop is reduced and consists of a comparatively long saccule with a small round opening. Five-six ducts with adjacent sorting tracts arise from the left lobe of the digestive gland within the sacculation.

The ciliation on the surface of the stomach was studied in newly opened individuals with the help of fine graphite and carmine particles. The largest concentrations of cilia in the Yezo scallop were noted on the surface of the perioesophageal ridge, the folds of the dorsal hood, and in the plicate sorting zone. The particles of graphite placed on the surface of the right part of the oesophagus are moved by the cilia to the apex of the right fold of the dorsal hood. An important role is played by the ciliated groove at the base of the oesophageal ridge, for it collects particles from the remaining part of the oesophageal ostium and the underlying regions of the stomach, and also conveys them to the apex of the righthand fold of the dorsal hood. A smaller portion of the particles finds its way into the sorting cecum of the stomach and, via the apex of the left fold of the hood, onto the right fold and then into the cecal end of the hood. Countercurrents (towards the cecal end of the hood and back) exist in the ciliated groove between the two folds of the dorsal hood. The particles placed on the left fold of the hood near the left sacculation find their way directly into the latter. All the particles from the plicate sorting zone of the stomach move toward the intestinal groove of the fore-intestine; the ciliated tracts of the apexes of the folds, their grooves and the tracts of the large and the small intestinal groove function as rejection tracts. The ciliary accumulations on the surface of the posterior sorting zone are very weak in comparison with those on the plicate part. They are directed mainly toward the marginal parts of the gastric shield. The ciliary accumulations of the right marginal part of the posterior sorting zone perform resorting functions, returning the graphite particles either to the sorting zone, or to the dorsal hood. Therefore, two main directions are noted on the surface of the stomach in the Yezo scallop, i.e. into the dorsal hood along the food receiving tract, and from the surface of the ciliated sorting zone along the rejection tract. Besides these main directions on the surface of the stomach, there should be quite a number of other resorting directions that ensure effective sorting of particles. We can only say that the resorting of particles takes place in the groove of the dorsal hood, in the posterior sorting zone, and on the surface of the thickened wall of the stomach above the right ducts.

6.2.2.1. Gastric shield

The gastric shield is lined with columnar cells 120-160 μm high, reaching 270 μm in height under the highest part of the shield. The epithelium rests on the thin basement lamina with its underlying layer of connective-tissue and muscle fibres, under which numerous hemal spaces are seen. The nuclei of the epitheliocytes have the typical rod-shaped form, and are found in the distal part of the cells. In the marginal parts of the shield, the nuclei lie at different levels of the epithelial layer. The entire perinuclear part of the cytoplasm of the cells is filled with a secretion in the form of granules, drops, strands and filaments. The epitheliocyte secretion of the shield is highly basophilic, has a strong affinity to staining with paraldehyde fuchsin by Gomori's method, and contains glycoproteins. The apical parts of the cells bear a perceptible ciliate brush border, and form clavate evaginations. The cuticular lamella is tightly adpressed to the apical ends of the cells, and consists of glycoproteins. The lamella is characterized by marked cross-lamination and longitudinal striation. The first apparently depends on the periodicity of the secretion processes of the lamella, and the second on the secretory activity of the individual cells. Separate granular-vacuolated cells are found in the marginal parts of the gastric shield. Their apical parts are expanded and packed with numerous light-coloured vesicles, granules and rods of a material with an affinity to toluidine blue. These cells are presumed to be mucous elements.

6.2.2.2. Sorting zone

The epithelium lining the plicate part of the sorting zone of the stomach forms regular folds and grooves. The cells are 140-200 μm high along the centre of the folds, and 30-50 μm high in the grooves. The cells are very thin, and widen only in the apical zone and near the nucleus. The apical ends bear a well-developed brush border and a well-developed ciliary apparatus. The cilia are about 11 μm long. The epithelium rests on the basement lamina with its underlying layer of connective-tissue and muscle fibres. This is followed by a layer of bundles of longitudinal and circular muscle fibres and numerous hemal sinuses. The basal part of the epithelial layer is characterized by spherical intraepithelial spaces filled with a fibrous material. The nuclei of the cells are oval, contain 1-2 nucleoli and distinctly granular chromatin, and are distributed in 7-10 rows at different levels of the epithelial layer. The part of the epithelial layer above the nucleus is characterized by the presence of indistinctly formed cells and different-sized vacuoles in the cytoplasm. Some of the vacuoles contain glycoproteins. In the specimens analyzed in spring, the vacuoles were yellowish-green, similar to the digestive vacuoles in the cells of the digestive gland. Apparently, excretory products with lipofuscin accumulate in these vesicles in spring. The second structural peculiarity of the epithelium in the ciliated sorting zone is the granularity of its cytoplasm, which is especially pronounced in the region of the root threads of the cilia, where the cytoplasm contains a high concentration of proteins. The brush border turns a dark colour when stained for proteins, and a medium or light colour when stained for polysaccharides. The cells in the grooves of the folds are distinguished from the epitheliocytes at the apices of the folds by a less vesicular cytoplasm and by a more developed ciliary apparatus.

Thus, the sorting zone is composed mainly of one type of cells, ciliated ones. The latter are polyfunctional, for in addition to the transport function (conveyance of food particles), they perform other functions as well, namely secretion and excretion of PAS-positive material and, possibly, proteins; it is also possible that the cells of the sorting zone are capable of directly absorbing digestive products from the lumen of the stomach. The developed brush border and the vesicular and fibrous nature of the cytoplasm are an indication of this.

It should be said in conclusion that lighter and dark cells are encountered in the epithelium of the centre of the folds. Threadlike pycnotic nuclei are found in the dark epitheliocytes, which suggests that they are the ageing elements of the epithelium.

On the whole, the histological structure of the posterior sorting zone repeats the structure of the plicate part. In this zone, however, we do not observe regularity of the folds and grooves, and the ciliary apparatus is far less developed. It is not excluded that other elements besides ciliated ones occur here, but it would be difficult to identify them at the optical level due to the large number of food particles on the apical surface of the layer.

6.2.2.3. Dorsal hood

The righthand and lefthand folds of the dorsal hood are formed by evagination of connective tissue into the lumen of the stomach, and are covered with very high epithelial cells (approximately 250 μm in the region of the folds compared with 50-100 μm at the bottom of the dorsal hood). Most of the epithelial lining is composed of ciliated cells with a well-developed ciliary apparatus (length of cilia 11 μm). The nuclei are distributed in 10-30 rows at different levels of the epithelial layer. The part of the cytoplasm above the nucleus is moderately PAS-positive, slightly basophilic; it is less granular and less vesicular than in the cells of the sorting zone. Furthermore, individual paraldehyde fuchsin-positive granules and fibrillation are observed in the cytoplasm. A high concentration of proteins is noted along the apical margin of the epithelial layer and in the well-developed brush border.

The epithelium of the bottom of the dorsal hood forms small folds because of the different height of the cells. The nuclei that make up the epithelium of the ciliated elements are oval, and are distributed in three rows in the basal one-third of the layer. The cytoplasm of the cells is basophilic. The apical parts are distinctly granular and at the same time vacuolated, and they contain proteins. Mucopolysaccharides are present in the vacuoles. Bulbar evaginations appear on the apical surface of the ciliated epitheliocytes, and separate into the lumen of the stomach by means of clasmatosis together with PAS-positive and basophilic-granular material. The ciliated epithelium of the bottom of the dorsal hood probably performs an active secretory function in the scallop. Large masses of rejected basophilic cells together with nuclei are found in the lumen of the stomach. Among the ciliated cells of the folds and bottom of the dorsal hood, we encounter sparsely distributed high threadlike mucous cells with glycosaminoglycans.

6.2.2.4. Large typhlosole

The large typhlosole in the Yezo scallop consists of a crest formed mainly by cells of different height, and a comparatively flat plateau, or expansion, of the typhlosole. The transition of the crest into the plateau is gradual. The cells are about 300 μm high at the apex of the crest, and about 160 μm on the plateau. The epithelium of the large typhlosole is composed of ciliated and narrowly specialized cells. The ciliated cells of the typhlosole are similar to the same elements in other parts of the stomach, i.e. they have a well-developed ciliary apparatus, brush border and granular cytoplasm; however, unlike the sorting zone of the stomach, the perinuclear cytoplasm here is vesicular only in some cells. The narrowly specialized elements of the typhlosole have the form of a keg or drum stick. The spherical or oval nucleus occupies a basal position, and it is often pycnotized. Depending on the ripeness of the secretion, the cytoplasm is either diffusely pigmented, or the dye is selectively absorbed by the granules or strings of secretion found between the vesicles. The secretion contains glycosaminoglycans and/or glycoproteins. This gives grounds for regarding these cells as unicellular mucous glands. The cytoplasm of the mucous elements react very intensely to Gomori's paraldehyde fuchsin stain. It is possible that the mucus of these cells has a more complex composition than in the mucous elements from other parts of the stomach. The secretion is discharged when the narrow apical tip of the cells is projected into the lumen of the stomach. The basal parts of the mucous cells of the typhlosole come into direct contact with the basal cells, enveloping them from both sides.

Basal cells are also comparatively common in the epithelium of the folds of the dorsal hood and in the posterior sorting zone of the stomach. They have a spherical shape, a nucleus with a small nucleolus, and a basophilic punctulate cytoplasm. In some cells we can see one, two or three processes extending to the basement membrane, less commonly into the apical zone of the layer. Small granules and vesicles are detected in the cytoplasm of the basal cells with the paraldehyde fuchsin stain. We also managed to observe the emergence of these granules into the intercellular spaces of the epithelium. However, the cytoplasm of many of the basal cells did not stain with paraldehyde fuchsin. Some cells are polyploidal, with two or with one very large nucleus. This combination of characteristics of the basal cells permits us to assume that they are nerve cells or neuroendocrine cells.

In addition to mucous and nerve elements, other narrowly specialized protein-rich cells are observed in the stomach epithelium of the Yezo scallop. They were found in ciliated epithelium, in a cross-section of the large stomach fold in specimens examined in June. A more accurate localization of these cells has not yet been established. The protein cells show an intensive and diffuse reaction to staining for total proteins with fast green. Their extended bodies are located in the central part of the epithelial layer, whereas the narrow apical ends cannot be seen.

One can assume that the protein cells play an important functional role which is directly related to the process of protein digestion in the stomach.

The structure of the stomach wall in the plicate part of the recesses with ducts is similar to that of the sorting zone. The structure of the nonciliated "pathways" of these zone is similar to the structure of the nonciliated groove of the digestive gland ducts, i.e. the epithelium here is composed of border cells. The typhlosoles, which separate the border epithelium of the "pathways" from the plicate part of the ducts, are formed in the same way as the typhlosoles of the ducts themselves, i.e. by ciliated cells of different height, which include a comparatively large number of mucous elements similar in their tinctorial properties to the mucous elements of the large typhlosole of the stomach.

The following conclusions can be made on the basis of our study of the histological structure of the stomach. The wall of its different parts is of the same structure on the whole. It consists of two principal layers, epithelium located on the basement membrane and fibrous connective tissue. Numerous hemal spaces and individual bundles of longitudinal and circular muscle fibres are found amidst the connective-tissue elements. In some cases, the basement membrane of the epithelium comes into direct contact with the hemal sinuses. A well-developed blood supply to the stomach wall and the presence of an abundant network of intercellular spaces in the basal parts of the epithelial layer may be an indication of direct transport of nutrients from the stomach into the blood-vascular system of the scallop.

The epithelial lining of the stomach is formed by ciliated cells (much of the stomach), cuticular cells (gastric shield), mucous cells (the large typhlosole, the typhlosoles of the nonciliated "pathways" of the ducts, less commonly in the rest of the stomach), nerve and neuroendocrine cells (mainly in the folds of the dorsal hood and the large typhlosole, and in the posterior sorting zone), border cells (nonciliated "pathways") and protein cells. The structural characteristics of the ciliated and cuticular epithelium point to their polyfunctional nature and, consequently, the organizational primitiveness of the stomach in the scallop. The clearly defined structurization of the perinuclear cytoplasm (vesicular and granular), the well-developed brush border, and the concentration of glycoproteins in both the latter and in the apical zone permit us to characterize the cells of the sorting zone as ciliated absorptive elements.

6.2.3. Digestive gland

The digestive gland is the principal organ of absorption, phagocytosis and intracellular digestion of food, and it performs a number of functions associated with digestion. The structure of the digestive gland of filter-feeding mollusks is well-researched (see Leibson, Usheva, 1979). The microscopic structure and the cellular composition of the digestive gland (Suzuki et al., 1968; Usheva, 1979) and the seasonal changes in its content of lipids and glycogen (Takahashi, Mori, 1971a, c) and its absolute mass (Fuji, Hashizume, 1974), as well as certain enzymes (Kozlovskaja, Vaskovsky, 1970), have been studied in the Yezo scallop.

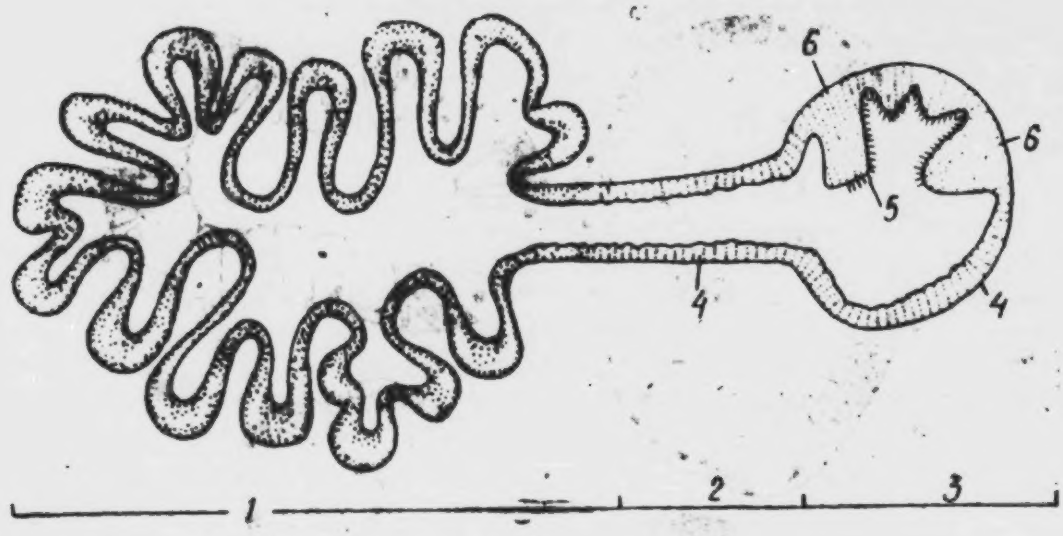


Fig. 28. System of digestive tubules running into a duct: 1 - longitudinal sections of tubules; 2 - longitudinal section of secondary duct; 3 - transverse section of main duct; 4 - border epithelium; 5 - ciliated epithelium; 6 - typhlosoles of duct

The digestive gland (Fig. 26) consists of numerous cecal tubules and their ducts. Approximately 30 large ducts connect the gland with the stomach. The large, or main, ducts branch within the gland, and break down into a system of smaller ducts which pass into very short secondary ones, into which the ostia of the digestive tubules open (Fig. 28). The space between the ducts and the tubules is filled with thin interlayers of connective tissue, glycogen-abundant muscle fibres, sinuses and lacunae of the hemal system. Under the basement membrane of the tubules, Suzuki noted a large number of blood capillaries. Around some of the large blood vessels, we encounter groups of tubules surrounded by a thicker connective-tissue layer and muscle fibres, as a result of which distinctive lobes with a vessel in the centre are formed in the organ; the transition of the wall of the tubule into the hemal sinus can sometimes be observed; all this point to the possibility of a direct contact between the tubules of the gland and the hemal fluid.

6.2.3.1. Digestive tubules

The digestive tubules in the Yezo scallop are simple or branching (Fig. 29), and lined with epithelium that rests on a thin basement membrane. Under it, we sometimes encounter individual muscle cells. The epithelium of the tubules is composed of light-coloured digestive and compositionally heterogeneous dark cells. Large secretory and smaller cambial elements are distinguished among the latter. Young transitional forms are found between the cambial elements and the specialized (digestive and secretory) cells (Usheva, 1979).

The digestive cells are large, prismatic, with a large nucleus occupying a basal position. Their apical margin bears a brush border, and the cytoplasm is filled with vacuoles differing in shape, size and colour, which comprise elements of the lysosomal system of intracellular digestion. The vacuoles readily stain for glycosaminoglycans and glycoproteins. The swelling of the apical ends of the cells and extrusion of their contents into the lumen of the tubule are characteristic of these cells. The fine subapical oxyphilic granularity stains for mucus, and reacts positively to total proteins and mucopolysaccharides (Usheva, 1979). Individual granules of glycogen and drops of lipids are also found in the cytoplasm.

As they age, the digestive cells undergo a number of changes. Yellowish-green residual bodies containing lipofuscin accumulate in their cytoplasm; as a result, they fuse into more compact spherules. At the same time, the cells grow lighter because of the colourless drops of lipids filling them, which fuse into a single large vacuole in the basal part. This leads to the swelling of the cells, and the compression and atrophy of the adjacent basophilic elements. The nuclei are pushed back toward the basement membrane or sides of the cells, and become deformed, after which they undergo pycnotization and lysis; such nuclei stain very poorly with Feulgen's method. Individual nuclei appear fairly viable on the background of the destructive cytoplasm. Near the bottom of the tubules, the ageing cells often form groups that protrude above the rest of the epithelium, and are distinguished from it by a lighter appearance. Some of these cells retain the wholeness of the apical margin with a well-defined brush border. Apparently, digestive cells that are completing their cycle can actively participate in the absorption of substances, primarily lipids. This function of theirs intensifies where they form groups, i.e. near the bottom of the tubules. On the other hand, breaks in the apical margin with the discharge of pigmented excretory spherules into the lumen are observed in other cells of this type.

Cells abounding in neutral lipids were detected in the epithelium of the tubules of the Yezo scallop by Suzuki and coauthors (Suzuki et al., 1968). However, judging from drawings, Yonge considers similar cells in *P. opercularis* to be old digestive elements with yellow excretory concretions. In our opinion as well, Suzuki's "lipid" cells are nothing more than digestive cells at the final stage of the life or functional cycle, which are actively participating in the processes of accumulation (e.g. lipids and glycogen) and excretion. This point of view has been confirmed by our observations on the state of the epithelium of the tubules in the course of the digestive cycle over a period of 24 hours. We found that if the digestive cells are scarce at the initial stages of the cycle, their number reaches one-third to one-half of the total cell content of the tubules at the end of the cycle.

The basophilic cells are diffusely scattered along the length of the tubule in crypt-like groups or singly. Approximately 10% of the total number of basophilic elements is made up of specialized protein-secretory elements (October). They are pyramidal or conical, large, with large nuclei containing light-coloured karyoplasm and a hypertrophied nucleolus. The perinuclear cytoplasm is highly basophilic and fibrillary, and reacts intensively to total proteins, RNA and PAS-positive substances. The apical parts of the cells are lighter, and filled with slightly pigmented vesicles. At the end of the digestive cycle, these parts are rejected into the lumen in the majority of basophilic cells, and the cells themselves acquire an irregularly cubical form, at the same time retaining a high degree of perinuclear basophilia and large nuclei and nucleoli. The enzyme-containing vesicles rejected with apical cytoplasm probably continue on into the stomach where they effect the cavitary stage of digestion. Direct discharge of the secretion in the form of basophilic spherules from the cells into the lumen of the tubule has also been observed in the scallop in spring. The ageing secretory elements collect excretory material in the perinuclear vacuoles.

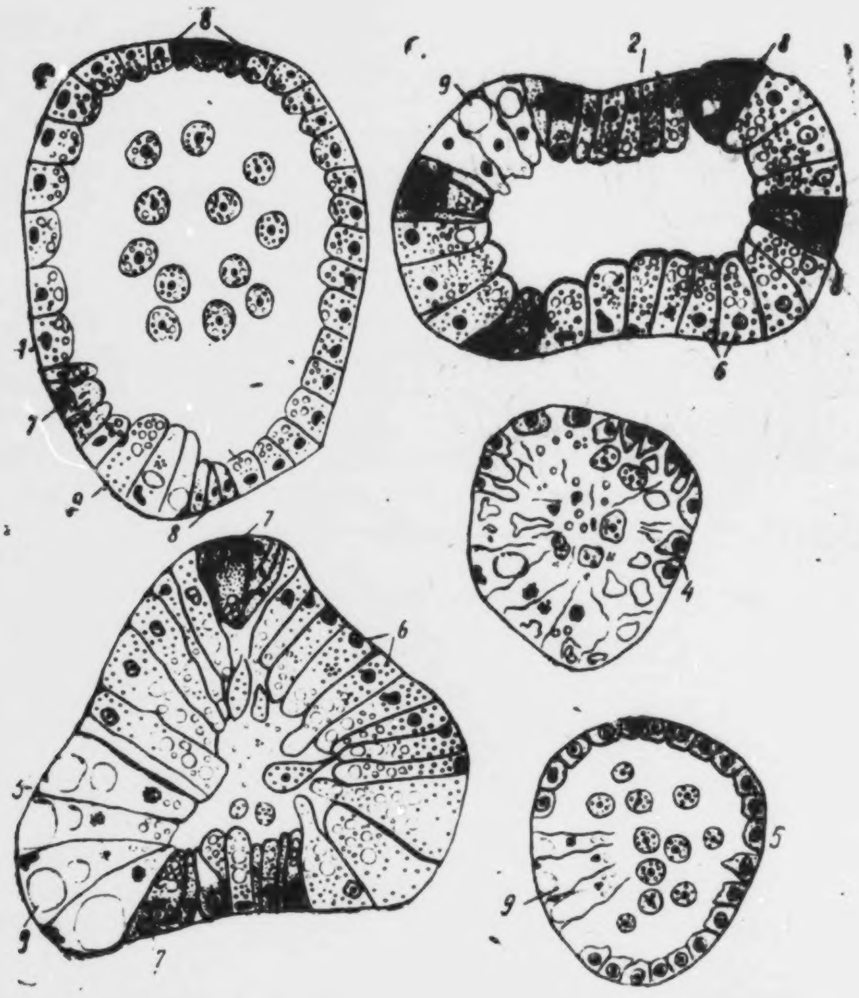


Fig. 29. Tubules at different stages of the digestive cycle: 1 - at rest; 2 - absorption; 3 - digestion; 4 - destruction; 5 - regeneration; 6 - digestive cells; 7 - secretory cells; 8 - cambial cells; 9 - loci of old digestive cells accumulating nutrients

Two varieties, cambial and vacuolated, should be singled out among the small basophilic cells of the epithelium of the tubules in the digestive gland of the Yezo scallop (Usheva, 1979). We regard the vacuolated ones as young forms, since transitional states between them and more mature digestive and secretory elements have been observed. The cambial cells are cylindrical or conical, and lack a brush border. Their nuclei vary from very small hyperchromatic ones to comparatively large ones with granular chromatin; among them, we encounter nuclei in a pre-prophase and prophase state, as well as nuclei initially labelled with ^{3}H-thymidine. The cambial elements in the epithelium of the digestive gland tubules of the Yezo scallop are randomly scattered with no specific sites of localization either in the corners or on the bottom of the tubules. These cells lie adjacent either to the basophilic secretory ones, or to the groups of old digestive cells. One can assume that, in the Yezo scallop, the specialized epitheliocytes of the tubules in the digestive gland are renewed by its own cambium.

In order to establish the regenerative potentials of the basophilic cells in the epithelium of the digestive gland tubules, it is important to trace its condition at different stages of the digestive cycle. Like other bivalves, specifically *P. maximus* (Mathers, 1976), the Yezo scallop displays five different conditions of the tubules, which correspond to the stages of the digestive cycle, namely dormancy, absorption and phagocytosis of food particles, digestion, disintegration and regeneration. At the dormant stage, the lumen of the tubules is large and round, and lined with very low prismatic cells; yellowish-green and colourless vacuoles are seen in the digestive cells; individual old light-coloured cells (far more abundant in July—August than during the rest of the year) are encountered in the bottom epithelium of the tubules; the basophilic elements consist of typical secretory and cambial cells. Germ cells and epitheliocytes (secretory and digestive) rejected at the previous stage of the digestive cycle are found in the lumen of the tubules. The intertubular connective-tissue interlayers are well-defined.

At the stage of absorption and phagocytosis, the lumen of the tubules is still fairly large, though somewhat smaller than at the previous stage; the epitheliocytes lining it are low-prismatic, with a well-defined brush border; the digestive cells have a clearly defined subapical granularity and an increased number of colourless vacuoles.

At the digestive stage, the lumen of the tubules is considerably smaller and irregularly shaped as a result of the swelling of the digestive cells in it, which now become high-prismatic and packed full of different kinds of vacuoles. The basophilia of the secretory elements increases drastically. The rejection of large fragments of digestive cell cytoplasm and their complete desquamation into the lumen of the tubules are observed. We note an increase in the number of old digestive elements swollen with lipid inclusions, which form groups on the bottom of the tubules; at the same time, the secretory elements adjacent to them become atrophied. The tubules at this stage are enlarged and come into close contact with each other; their basement membrane becomes imperceptible, and the connective-tissue interlayers between them decrease significantly or even disappear.

At the next stage of the digestive cycle, disintegration of the tubules, their lumen is completely filled with fibrous rejection fragments of cytoplasm and yellowish-green residual bodies containing lipofuscin. At the same time, one of the sides of the tubules appears to be lined with strongly basophilic cells with large nuclei and nucleoli, and what appear to be broken off apical ends. In the course of the regenerative stage, these cells flatten out and spread over the entire perimeter of the tubule. They later acquire a conical form, and their cytoplasm becomes less basophilic, with individual vacuoles appearing in it. The further differentiation of these cells progresses in two directions; the number of digestive spherules increases in some cells, while the perinuclear basophilia characteristic of the secretory elements increases in the others.

Two modes of destruction and subsequent regeneration of the tubular epithelium are noted in the Yezo scallop. With the first mode, only individual groups of digestive and secretory elements undergo destruction, not the entire tubule as described in the literature for the majority of studied mollusk species. Separating from the tubules into the appropriate connective tissue, these groups apparently undergo either definitive necrosis with the utilization of catabolites by the migratory elements, or intracellular regeneration with subsequent incorporation of them into the epithelium of the adjacent tubules. With the second mode, we observe mass destruction of the tubules with the loss of the majority of specialized epitheliocytes; cambial elements, on the other hand, survive, and their proliferation ensures the regeneration of the entire epithelial lining. The first mode of tubule regeneration is more pronounced in December—April, and the second mode in July—August.

It has been established that many of the bivalve species are characterized by cyclicity of feeding and digestion, associated with the tidal and diurnal rhythms in nature. The digestive cycle in these mollusks manifests itself specifically in the synchronization of the condition of the digestive gland tubules which function in a specific single- or two-phase rhythm for the given species and given water area. For example, a two-phase feeding and digestive cycle extending over two tidal cycles has been described in the typical sublittoral species *P. maximus* (Mathers, 1976); according to Mathers, about one-half of the digestive gland tubules are found at the stages of absorption and digestion at any time of the day and night, whereas the second half are at the stages of disintegration and regeneration. The digestive cycles in the Yezo scallop are determined mainly by the diurnal rhythm, as indicated by the diurnal variations in the rate of filtration, which peaks during the night (Sadykhova, 1973). Our histological analysis of the condition of the digestive gland in adult scallops (March) and one-year-olds (August) over a 24-hour period has shown the following. At any time of the night and day, the digestive gland is found to contain tubules at different stages of the digestive cycle, i.e. no clear photoperiodization of their condition is noted. At the same time, because of significant individual variations, it is difficult to decide which condition of the tubules prevails at this or that time. It is especially difficult to delimit the stages of absorption and digestion, and also the stages of disintegration and regeneration; they are so closely interrelated that they can occur simultaneously in one and the same tubule. Tubules at the dormant stage were the least common; they were encountered singly, predominantly in the central zone of the gland near the stomach. This is an indication of the high functional activity of the digestive gland and, therefore, the digestive system as a whole in the Yezo scallop during the indicated seasons (March—August).

The systematic year-round observations carried out by us with 3-year-old Yezo scallops from Posyet Bay have enabled us to characterize the seasonal changes in the digestive gland of this species. In autumn (October), for example, the gland contains an approximately equal number of tubules at the stages of absorption and digestion on the one hand, and at the stages of disintegration and regeneration on the other. In winter (December—February), the number of tubules at the stages of absorption and digestion increases drastically (up to 70-80%), reaching the maximum (90%) in March—beginning of April. During the post-spawning period (July—August), we note a significant prevalence of disintegrating and regenerating tubules; at the same time, the number of old digestive cells filled with lipid drops increases at the bottom of the tubules.

According to Suzuki and coauthors, the number of cells that store up lipids in the digestive gland tubules of the Yezo scallop amounts to only 25-30% (of all the epithelial cells) in winter, whereas it increases sharply (to 53%) after spawning, in June, and reaches 75% with parallel destructive changes of the secretory and basophilic elements in August (Suzuki et al., 1968). Takahashi and Mori have also shown that, in summer, the Yezo scallop accumulates large quantities of neutral fats which decrease significantly with the onset of gametogenesis (October), and then increase gradually, reaching the maximum towards the following post-spawning period.

It is quite probable that the destruction of the digestive gland tubules observed by us in the scallop during July—August was due to the massive deposits of nutrients, primarily lipids, in them. In other words, the function of deposition at this time becomes the predominant one for the digestive gland; the accumulated reserves are utilized during active gametogenesis which begins in autumn, following the period of sexual inactivity. There is, however, another probable cause of the destruction of the digestive gland tubules observed in August, the damaging effect of the high temperature of the water during this period. As shown for other species of invertebrates, a high water temperature can inhibit a number of body functions. It should be said that the destructive changes in the digestive gland coincide in time (July—August) with the disturbance of linear growth in the scallop (Silina, 1976, 1977).

6.2.3.2. Ducts

The main ducts of the digestive gland are spherical in cross-section. Their interior lumen is divided by large typhlosole-like folds into two grooves. One of the grooves is lined with border cells, and, as considered for all bivalve mollusks, is an incurrent tract which takes the food particles from the stomach into the digestive tubules. The second groove is lined with cells of different height which form a clearly defined rugosity, and is the excurrent tract which takes the residual bodies of intracellular digestion and the rejected cells of the digestive tubules into the stomach. Under the basement membrane of the ducts, unlike that of the digestive tubules, there is a layer of muscle fibres which increase in definition with the size of the ducts.

The ciliated cells of the main ducts are characterized by a well-developed (especially at the apices of the folds) ciliary apparatus and a distinctly basophilic, granular or reticulate-vacuolated cytoplasm which reacts weakly or moderately to polysaccharides and to total proteins; these reactions intensify near the apical margin where the granularity is finer and denser. The elongated nuclei of the cells are located at a different height in the central part of the layer. Directly above the nuclei, especially in the cells found in the centre of the fold, we encounter individual vacuoles which react to the mucus stain. The vacuoles often contain a yellowish material, probably residual products of cell activity. Highly light-refractive excretory granules have been described in the ciliated cells of the ducts in *P. opercularis* (Yonge, 1926). In the Yezo scallop, sparse degenerating cells with pycnotic nuclei are encountered predominantly among the apical ciliated cells of the folds. Since pycnoses are rare and cell rejection into the lumen of a duct has not been observed, it is difficult to tell whether the dead elements desquamate, or undergo lysis within the layer. Individual granules of glycogen are found in the cytoplasm of ciliated cells.

The border epithelium of the main ducts consists of loosely distributed light-coloured cells that are wider than the ciliated cells. Their nuclei are more often oval and hypochromatic, with 1-2 large nucleoli. The cells are characterized by a granular and oxyphilic apical zone of the cytoplasm, as well as by the presence of large vacuoles that fill its larger part, and a well-defined high brush border; the vacuoles are slightly oxyphilic, and react positively to total proteins and glycoproteins. The apical parts of the cytoplasm of many of the border cells form bulbar evaginations into the lumen of the duct, undergoing rejection by clasmatosis; this gives the margin of the border epithelium its characteristic frothy appearance. There are also many cases where entire cells are extruded into the lumen. In autumn, the border epithelium of the ducts reacts strongly to mucopolysaccharides. In addition to diffuse staining of the cytoplasm (especially the apical margin), numerous granules and globules of glycogen are found. The function of the glycogen in the epithelium of the ducts is not quite clear; perhaps the glycogen coming from the stomach is absorbed and reutilized here. The intensive secretion of PAS-positive material by the border epitheliocytes of the ducts during the autumn (with simultaneous destruction and rejection of some elements) points primarily to their high functional activity and likely participation in the digestive processes. We note an unusually high (compared with other parts of the intestinal tract) brush border in the epithelium of the incurrent tract, which is also an indication of active metabolic processes. The contribution of the border epithelium of the digestive gland ducts to the absorptive and digestive processes has been shown for *Chlamys opercularis* (Reid, 1968) and *P. maximus* (Mathers, 1976), in which the epithelium of the ducts was found to contain enzymes of intracellular and perimembranous digestion, namely esterases and acid and alkaline phosphatases. A high content of phosopholipids was found in the epithelium of the ducts in the Yezo scallop (Takahashi, Mori, 1971b), an indication of a well-developed cell-membrane apparatus. Apparently, the functions of the ducts are not limited solely to passive transport of food particles from the stomach to the digestive gland and back, but have far more to do with digestion. Though there is no question about the secretory activity of the border epithelium of the main ducts in the Yezo scallop, we must continue our research in order to establish the nature of the enzymes and their exact localization. It is not excluded that the PAS-positive secretion of the border epithelium is linked with the secretion of mucus which facilitates the transport of food particles. Mucocytes in the epithelium of the ducts are rare in this species, and are usually localized in the region of the typhlosole-like folds; their secretion contains a mixture of glycosaminoglycans and glycoproteins.

The secondary ducts, which are short and branching, form the transition between the main ducts and the digestive tubules. The epithelium lining them, low-cylindrical with a single-row arrangement of spherical nuclei, is the direct continuation of the border epithelium of the main ducts, and is similar to it in a number of morphological and histochemical characteristics. Its cells also have a well-developed brush border, are granular in the subapical zone, and contain granules of glycogen and vacuoles in the cytoplasm (Usheva, 1979). However, the secretory activity of this epithelium is far more weakly defined. Migratory elements are often detected in the lumen of the secondary ducts.

6.2.4. Intestine

The intestine in the Yezo scallop is a fairly long (20 cm in 3-year-olds), slightly convoluted V-shaped tube (Fig. 26). It consists of three structurally and functionally different parts, namely the fore-intestine (or gastric intestine), the recurrent intestine, and the hind-intestine (rectum). The gastric intestine extends from the lower ventral wall of the stomach, and is embedded in the digestive gland, but at the level of the foot goes into the gonad; from about the middle of the gonad, the intestinal tube rounds off toward its free end where, curving sharply, it returns to the digestive gland as the recurrent intestine; perforating the ventral part of the gland, it then emerges from it as the hind-intestine, or rectum; the latter pierces the wall of the pericardial sac and ventricle of the heart, descends along the posterior surface of the adductor, and ends in a funnel-shaped anus which lies freely in the mantle cavity. As we can see, the course of the intestinal tract of the Yezo scallop is similar to that of *P. maximus* (Dakin, 1908).

The fore-, or gastric, intestine is a tube with two processes, or typhlosoles, which divide its lumen into two inequal grooves, a larger one, the sac of the crystalline style, and a smaller one, the intestinal groove. A structurally unified intestinal groove and style sac is regarded as a primitive organizational feature (Dakin, 1908; Owen, 1974); they are usually separate in the more highly organized mollusks. The crystalline style is a hyaline, translucent enzyme-containing rod. Its thickened end with a mass of mucous food particles wound on it is located in the stomach; from here, the style runs along its sac to the end of the gastric intestine, where it is usually soft and partially dissolved. Depending on the season, the style can be whitish, yellowish, greenish, or colourless. The style reacts positively to PS-Schiff material and total proteins. A cross-section of the style shows concentric lamination. The typhlosoles of the gastric intestine are formed mainly by cells of different height and to some extent by small evaginations of connective tissue. Shallow grooves are found on the apices of the typhlosoles, especially in old scallops. The central parts of the typhlosoles in a live intestine are usually bright orange-reddish brown, the intensity and shade of pigmentation varying with the seasons. Visually, the pigment in the epithelium of the typhlosoles may be granular, or finely dispersed. The epithelium of the intestinal groove is usually unpigmented, while the epithelium of the style sac has a grayish-brown stripe in the part bordering on the small typhlosole. At the level of the posterior one-third of the gonad, the dimensions of the typhlosoles and the intestinal groove decrease, and high cristate regular longitudinal folds appear in the epithelium of the style sac; these folds are composed of cells of different height with small connective-tissue papillae. This type of contour also extends onto the beginning of the recurrent intestine, and then it smooths out. Perhaps the function of this deep rugosity of the transitional zone is to form the fecal strings, since only individual particles are seen in the mucous flow of the intestinal groove (initial segment), and long strings of particles are already noted in the recurrent intestine. Depending on its content of detritus, the recurrent intestine has the form of a simple tube with a single triangular, irregular or oval lumen. Here we usually observe a groove composed of 15-30 low-cylindrical cells bounded by small folds, the remains of typhlosoles. This is a reduced intestinal groove which continues in the form of a distinctive ciliated canal into the hind-intestine (rectum). The morphology of the latter is, on the whole, similar to that of the recurrent intestine; it is distinguished from it by the presence of its own membrane and a sharply defined rugosity of contour. As a rule, it has 3-5 large longitudinal folds with a small connective-tissue papilla and a mass of smaller apical ones formed by cells of different height (200-300 μm on the apices of the folds and 100-150 μm, less commonly up to 20-30 μm, in the spaces between them). The appearance and nature of the rugosity are of a sporadic nature, and depend on the detritus content of the intestine and, perhaps, also on the change in its contour during preparation and fixation. The epithelium of the entire intestinal tract is characterized by a clearly defined capacity to gather in transverse folds like an accordion due to the contraction of muscle fibres. With prolonged contraction of the adductor, the gonad contracts simultaneously with the intestine, decreasing to one-third of its length.

The intestinal wall in the scallop consists of three main layers, a thick epithelial layer, a very thin inner layer of circular muscle fibres, and a layer of loose connective tissue (with numerous hemal sinuses); the latter layer reaches its highest degree of development in the hind-intestine, where it is pierced by bundles of muscle fibres extending in different directions. The hind-intestine has an additional outer muscular layer consisting of ordered bundles of longitudinal and circular fibres with groups of connective-tissue cells between them, and it is covered by a layer of low-cylindrical epithelium with numerous mucocytes. The epithelium rests on the basement lamina which readily stains with alcian blue and aniline blue, and forms numerous invaginations into the layer; it consists of the basement membrane and a layer of orderly arranged collagen fibres (Usheva, 1983). As it becomes thinner in the region of the typhlosoles and connective-tissue papillae, the basement membrane acquires the form of a wide diffuse membrane. Germ cells, apparently migrating from the connective tissue to the epithelium, are common for these parts.

The epithelium lining the intestinal tract is one-layered, tall-prismatic, ciliated epithelium with multirow arrangement of the nuclei. The epithelium of the crystalline style sac of the intestinal groove and the base of the folds of the recurrent and hind intestines is the shortest, and the epithelium of the typhlosoles and the centre of the folds of all the regions is the tallest. The boundaries between the cells are observed only in the apical zone; the nuclei form a clearly discernible nuclear "layer" in the central part of the epithelial layer, which constitutes one-half or two-thirds of its height. The epithelium of the style sac is 1—2-row epithelium, and that of the intestinal groove 2—3-row epithelium, whereas the nuclei in the epithelium of the typhlosoles, the recurrent intestine and the hind intestine are arranged in 10-12 rows and more. The lining epithelium is composed of ciliated and mucous cells throughout. Furthermore, electron-microscopic examination has shown that the hind intestine contains finely granular elements, probably of a neuroendocrine nature (Usheva, 1983). In the epithelium of the typhlosoles, we sometimes encounter individual coarsely granular, brightly pigmented cells which may be macrophages. Migratory elements are detected in the epithelium. The ciliated epitheliocytes, which make up most of the layer, are highly heterogeneous; among them we also encounter ciliated-secretory cells and cells transitional to mucous cells. The ciliated cells are high-prismatic (typhlosoles, recurrent intestine, hind-intestine) or low-prismatic (intestinal groove, crystalline style sac, ciliated grooves of recurrent and hind intestines). As a rule, their apical parts are expanded, and bear a well-developed ciliary apparatus and a brush border. The highest degree of development is observed in the ciliary apparatus of the epitheliocytes of the crystalline style sac, where the length of the cilia constitutes one-third of cell height, the basal bodies form a well-pigmented border, and their rhizoplasts go far into the cytoplasm, often reaching the nuclei. The ciliary apparatus of the epitheliocytes is poorly defined in the rest of the intestinal tract; the cilia in the intestinal groove and in the recurrent and hind intestines are often destroyed during fixation, though their basal bodies can be discerned quite well.

As shown by an electron-microscopic study of the epithelium of the hind intestine in the scallop (Usheva, 1983), the ciliated cells bear 4-17 cilia and up to 40 microvillae. Many large mitochrondria and multivesicular and residual bodies are found between the rhizoplasts of the cilia. Individual bordered vesicles, microtubules and microvesicles are encountered near the apical margin. Light and dark ciliated cells are clearly visible, and large bundles of fibrils, apparently belonging to the internal skeleton of the cells, are present in the central and basal parts of the cells. The perinuclear cytoplasm abounds in free and aggregated ribosomes. Golgi's complex and an irregular endoplasmic reticulum with highly expanded cisternae are comparatively well-developed in the ciliated cells.

The nuceli of the ciliated cells in the intestinal epithelium of the scallop are highly polymorphous and differ in optic density. For example, the nuclei in the region of the typhiosoles and the centre of the folds of the recurrent and hind intestines are usually elongated, rod-shaped, in old cells to the point of being threadlike and pear-shaped. In the epithelium of the crystalline style sac, the nuclei are larger, oval or spherical, with a low degree of optic density after staining by the Feulgen method. The spherical nuclei of the intestinal groove are smaller and more closely spaced; their optic density is significantly higher than in the nuclei of the epitheliocytes in the other parts of the intestine. Depending on the ratio of condensed and dispersed chromatin, several types of nuclei can be distinguished.

In the ciliated cells of the intestinal epithelium, the apical cytoplasm is typically granular and vesicular; the largest perinuclear vacuoles are encountered in the cells of the intestinal groove. A large number of vesicles of different size with electron-light contents is found in the apical zone of the hind-intestine (Usheva,1983). In ultrathin sections viewed under a light microscope, epitheliocytes are often found to contain apical clavate evaginations, some of which contain the basal bodies of cilia. Secretion is of the macroapocrine type, by clasmatosis; along with particles of undigested food, colourless or pale-coloured vacuoles stained for polysaccharides and proteins are found in the intestinal lumen. The presence of secretory activity in the ciliated epitheliocytes and its intensity are subject to individual variations which probably reflect the stage of the digestive cycle. This activity is characterized by a clearly defined locality, i.e. if secretion is taking place in certain parts of the intestine, the other parts of the intestine are free of it. Secretory activity also undergoes seasonal variations, i.e. it is highest in spring (from March to June), lowest in winter, and moderate to high in some individuals during the summer—autumn period. With an increase of secretory activity in the ciliated cells, the number of vesicles increases, and the apical highly granular parts of the cytoplasm react more intensively than at other times of the year to staining for glycoproteins.

Secretion from the ciliated cells (by clasmatosis) is most commonly observed in the intestinal groove, recurrent and hind intestines, and less commonly in the typhlosoles. In the epithelium of the crystalline style sac, a number of seasonal variations of the epitheliocyte cytoplasm point to their secretory activity, though no obvious secretion is noted. During the spring months, for example, the cytoplasm of the cells is markedly vesicular, the concentration of glycoproteins increases (especially in the apical ciliated zone), and the basal parts of the cells narrow drastically, which leads to the appearance of numerous large intercellular spaces. During this period, many of the cells desquamate into the lumen of not only the fore-intestine, but also the recurrent intestine; large portions of desquamated epithelium of an unusual white colour and defects of the layer can be discerned in the style sac even by the naked eye. Cells with an empty cytoplasm and pycnotic or lysing nuclei are often observed in the epithelium. After staining with acridine orange, the chromatin of many of the nuclei of the style sac epitheliocytes luminesces red instead of the usual green, which is an indication of an irreversible degenerative process.

As we know, the crystalline style of filter-feeding bivalves contains a number of enzymes primarily of the amylolytic series, which are secreted into the lumen of the stomach when the style is rotated against the gastric shield. The literature contains the most contradictory opinions regarding the formation site of the style itself (its glycoprotein matrix and enzymes). The data derived for the Yezo scallop is significant evidence that the style forms as a result of the secretory activity of the epitheliocytes of the style sac and adjacent parts of the typhlosoles.

The part of the large typhlosole adjacent to the style sac merits special attention; its epithelium consists entirely of ciliated secretory elements. The latter are characterized by a highly basophilic foamy cytoplasm which reacts to RNA and glycoproteins. Their nuclei are elongated, often dumbbell-shaped or twisted; they form a characteristic "palisade" along the basement membrane. The nucleoli are usually larger than in the usual epitheliocytes. In some of the cells, the apical ends filled with secretion undergo macroapocrine rejection into the intestinal lumen. The intensity of staining and secretion from the ciliated secretory elements of the typhlosole varies significantly, probably with the stages of the digestive cycle.

In addition to the two varieties of elements described above (ciliated and ciliated secretory), cells transitional to mucous cells are quite often observed in the epithelium of the intestinal tube. They are similar to the ciliated epitheliocytes in form, the morphology of the nuclei and the presence of a ciliary apparatus, but they are distinguished from them by a basophilic cytoplasm containing RNA and mucopolysaccharides. In semithin sections of the epithelium of the hind-intestine, a brush border was noted in these transitional elements, and a few small granules similar to those of the mucous elements were found between the terminal filaments of the cilia.

Specialized mucous cells are encountered throughout the intestine, with the exception of the crystalline style sac. The bodies of the mucocytes usually occupy a basal position, and are flask-shaped, conical, and less commonly cylindrical. Their nuclei are found along the entire height of the epithelial layer, but most commonly in its basal region where they are fairly large, with a large nucelolus. Depending on its ripeness, the secretion of the mucous cells may be foamy, vesicular or granular; extrusion of it into the lumen is macroapocrine. The mucous secretion is easily washed out during the processing of material (especially after aqueous fixatives), and then only spherical vacuums with altered nuclei are seen in the epithelium. The secretion of mucocytes of the intestinal tract contains glycosaminoglycans and glycoproteins. The mucous cells are distributed singly, or in small groups of 2-5 cells. In the basal parts of the typhlosoles, the accumulation of mucocytes (containing glioproteins) forms a distinctive endoepithelial glandular area.

The number of mucous cells in the epithelium of the intestinal tube of the Yezo scallop, the intensity of their secretory activity and the composition of the secretion undergo seasonal variations. In January, for example, we note a large number of young forms of mucocytes with basophilic cytoplasm, as well as more mature ones containing mainly glycosaminoglycans; during the spring—summer period, the number of mucocytes with a mixed secretion increases drastically; in August—September, cells containing neutral mucus prevail. Perhaps these changes in the type of mucus reflect the seasonal changes in diet (specifically the phytoplankton/zooplankton ratio). The highest secretory activity of mucocytes is noted in spring. During this period, pycnoses of their nuclei, especially in the epithelium of the intestinal groove, are common.

The epithelium of the recurrent and the hind intestines of the Yezo scallop also contains another type of glandular elements, namely granular cells. The number and size of these cells and the intensity of pigmentation of their granules undergo significant individual and seasonal variations. Granular elements are found in the intestinal epithelium of the scallop from November to May; they are not seen during the rest of the months, possibly because of a change in the tinctorial properties of their secretion. Granular cells are abundant in winter; the cell bodies are fairly large, conical or cup-shaped; in April—May, they are narrowly cylindrical, and are encountered less frequently. The nuclei of the granular epitheliocytes are not confined to a strict locality; they are encountered along the entire height of the layer. Morphologically, they are very similar to the nuclei of ciliated cells, but they are less elongated. Young granular cells are ciliated, whereas mature ones are nonciliated, and their apical ends swell out into the lumen, being at the stage of macroapocrine secretion. At the early stages of the secretory cycle, the cytoplasm in the peripheral and basal parts is usually nonhomogeneous, and contains mildly basophilic, indistinctly formed granules. The more mature secretory granules are dense, nonbasophilic, and fill the whole cell. The secretion of granular cells is slightly eosinophilic, contains proteins and bound lipids, but does not react to mucus. Therefore, the described cells secrete lipoproteins. Their function is still unknown.

The eosinophilic granular cells described in the intestinal epithelium of some bivalve species are rarely encountered in the Yezo scallop; among the specimens examined by us, they were found only in 4—5-year-old scallops in November. The similarity of the eosinophilic cells and granular elements are remarkable. It is quite likely that they are variants of the same cell type; however, their tinctorial properties differ during the different seasons; the eosinophilia of the granules points to the possible accumulation of a protein component in them.

In ultrathin sections, the epithelium of the hind-intestine was found to contain solitary finely-granular elements which we interpret as neuroendocrine elements (Usheva, 1983). The size, the characteristic peripheral rim ("halo") of these granules, their relationship with the tubular elements of Golgi's complex, and their highly developed system of microtubules and fibrils are similar to those described in the literature for the insulin-type cells of the intestinal epithelium in certain mollusks; however, the structure of the basal parts of the finely granular cells is typical of the terminal zones of neuroendocrine cells. The presence of this type of cells in the intestine of the Yezo scallop as well prompts us to assume that they play a major role in neurohumoral regulation of the digestive processes in the intestine.

In the Yezo scallop, the seasonal changes in enterocytes affect not only their secretory activity, but also other parameters such as the height of the epithelial layer, the sizes of the cells and their nuclei and nucleoli, the optic density, and the degree of chromatin condensation. For example, the height of the epithelial layer of the hind-intestine is at its maximum during the winter—spring period (January—April); it sharply decreases in May—June, and even more in

August (the period of maximum seawater temperatures); it begins to increase in October. The height of the epithelium in the recurrent intestine reaches its maximum in March; the average and similar values are observed in January, April, May and October, and maximum thinning of the epithelium coincides with the period of greatly reduced secretory activity (July—August).

The nuclei and nucleoli of epitheoliocytes in spring (March—May) are approximately twice as large as in the summer—autumn period, and the basophilia of the nucleoli increases significantly. The synthetic activity of the intestinal epitheliocytes intensifies in spring, which leads to marked hypertrophy of the epithelial layer. The accumulation of various products of residual metabolism in the apical cytoplasm of the cells is further evidence of increased synthesis. In summer—autumn, formations of this type are noticeably rarer. The observed intensification of specific syntheses in the intestinal epithelium of the scallop in spring is apparently due to the activation of feeding and digestion during this period. According to Takahashi and Mori, the main storing organs in the Yezo scallop are the adductor muscle for glycogen, the digestive gland for neutral lipids, and the intestinal epithelium for phospholipids (particularly abundant there during the post-spawning period) (Takahashi, Mori, 1971a, b). In August, the condition of the intestinal epithelium differs in many ways from its condition in spring. Among other things, both the nuclei and the nucleoli grow considerably smaller with a parallel increase in colour density.

Thus, the intestinal epithelium of the scallop is composed of ciliated, ciliated secretory, transitional-to-mucous, mucous and granular cells, as well as neuroendocrine elements. The ciliated epitheliocyte is the principal cell type. These cells are polyfunctional, for in addition to the transport function, they carry out a number of specific syntheses; however, the extent of their differentiation is insignificant. The morphology of the epithelial layer and the secretory activity of the cells undergo significant seasonal variations.

7. FEEDING

7.1. Composition of food

The first investigations to study the composition of the food consumed by the Yezo scallop were carried out in Peter the Great Gulf by A. Bazikalova (1930) who found diatomaceous algae, invertebrate eggs, bell animalcules, silicoflagellates, and very rarely small copepods and detritus in the stomach of the mollusk. Zhyubikas (1969) later found that the stomach contents of the Yezo scallop in the Aniva Gulf and in the S Kurile shallows consisted of organic detritus with bottom-dwelling diatoms (predominantly *Navicula*), as well as the planktonic *Destephanus speculum* . No detritus was found in the stomachs of the Yezo scallop from the Busse Lagoon; the main food consisted of planktonic algae and the remains of zooplankton and the tintinnian *Helicostomela subilata*..

Investigation of the feeding of the Yezo scallop in the water area of Popov Is. has greatly expanded the list of species consumed by the mollusks (Mikulich, Tsikhon-Lukanina, 1981).

One hundred and sixty-one species were identified in the contents of the digestive tract of the Yezo scallop; 94 of them were unicellular algae, and 67 were animal species; spores, eggs, detritus and mineral particles were also found.

As for the total number of forms (Fig. 30), diatoms take first place with 68 species, followed by protozoans (mainly bell animalcules) with 41 species, peridineans with 22 species, crustaceans 15 species, mollusk larvae 5 species, silicoflagellates 3 species, rotifers 2 species, and other types represented by one species. However, of the large number of organisms encountered in the digestive tract of the scallop, only one-third (28.6%) were of significant food value; of these organisms, algae and animals constituted 25 and 21 species (15.5% and 13.0%) respectively.

Detritus was present in the digestive organs of all the specimens, and constituted a significant part of the food bolus (30-70%). The detritus always included various amounts of a liquid granular plasmic substance which was impossible to separate from the remains of decaying plants and animals. The basis of this substance could have been formed by glabrous flagellates from the group of peridinean unicellular algae which were often highly abundant in the plankton. One can assume that the digestive organs of the scallop rapidly convert the glabrous flagellates into a granular plasmic substance which is then mixed with detritus.

Fairly significant time- and space-related changes are noted in the composition of the food consumed by the Yezo scallop.

In May and June, for example, detritus comprised the bulk of the food (60-70%) consumed by the 2—9-year-old scallops of Starka Strait in Peter the Great Gulf; prevalent among the algae were various species of *Coconeis* , especially *C. scutellum* , as well as *Dinophylus acuta* and *Protoceratium areolatum* ; in May, the animal species were represented by bivalve larvae, and in June, infusorians *Helicostomela longa* and *H. subulata* , crustaceans of the species *Evadne nordmani* , small copepods and their nauplii prevailed over the algae. Detritus also prevailed (60-70%) in the food consumed by 6—11-year-old scallops in May. This was supplemented mostly by animal species, mainly the larvae of polychaetous worms and small copepods; *Protoceratium areolatum* was the predominant algal food.

Detritus played a smaller part (30-50% of the food content) in July and August in one-year-old cultivated scallops from the same area. The diversity of plant and animal food organisms was actually identical, but animals prevailed over algae. The animals included a large number of *Helicostomela longa* , water fleas of the species *Penilia avirostris* , as well as small copepods of the species *Oithona brevicornis, O. similis* and their nauplii; the algal food included *Protoceratium areolatum* , as well as *Ditylum brightwelli* and *Thalassiothrix frauenfeldi* . The bulk of the food consumed by the Yezo scallop in August consisted of detritus (70%); various algae and animals were encountered in small amounts.

In September and October, the relative content of detritus in the digestive tract of a one-year-old scallop amounted to 30-50%. The prevalent foods were algae which included a large number of *Chaetoceros* species, especially *C. affinis* , as well as *Ditylum brightwelli, Rhizosolenia alata, Thalassiothrix frauenfeldi* and *Skeletonema costatum* ; the animal foods recorded during this period consisted of a numerous bivalve larvae and a smaller number of *Oithona brevicornes* and copopod nauplii.

In August, detritus constituted 60% of the food consumed by 7—13-year-old scallops in the western part of Popov Is. *Protoceratium areolatum* and *Skeletonema costatum* prevailed among the algae, and *Helicostomela longa, H. subulata* and *Penilia avirostris* were among the animal species consumed by the Yezo scallop.

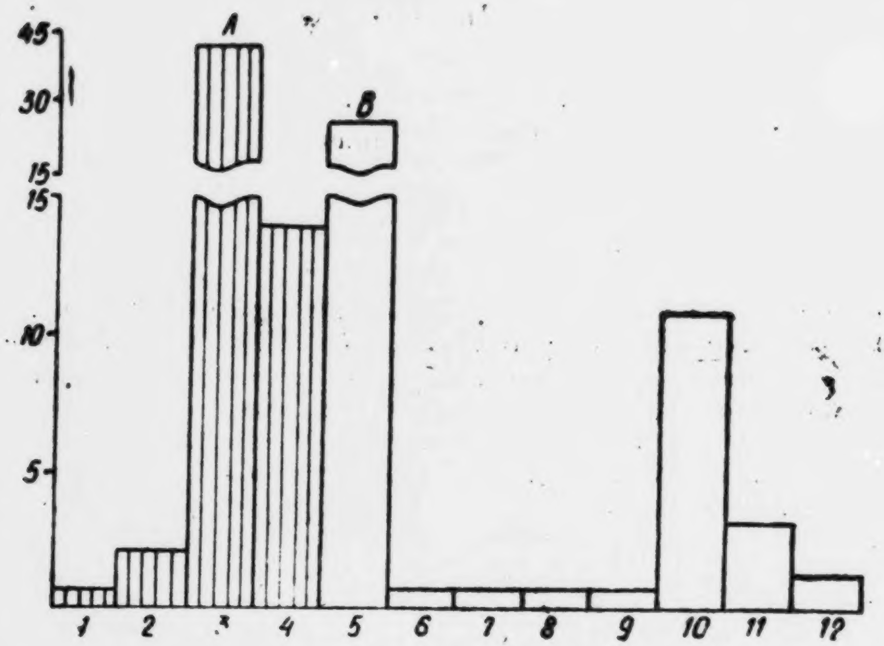


Fig. 30. Content of algae and animals in the diet of the Yezo scallop. A - algae, B - animals; 1 - Cyanophyta, 2 - Chrysophyta, 3 - Bacillariophyta, 4 - Pyrrophyta, 5 - Protozoa, 6 - Coelenterata, 7 - Plathelminthes, 8 - Nemathelminthes, 9 - Annelida, 10 - Arthropoda, 11 - Mollusca, 12 - Rotatoria. X-axis - taxa, Y-axis - their percentage of the food consumed by the scallop

Thus, detritus constitutes the bulk of the food consumed by the Yezo scallop in the vicinity of Popov Is.; this is supplemented by algae, mainly diatoms and peridinians, as well as infusorians *Helicostomela longa* and *H. subulata* , the water flea *Penilia avirostris* , small copepods of the species *Oithona similis* and *O. brevicornis* , copepod nauplii, and the larvae of mollusks and polychaetous worms.

The sizes of the organisms consumed by the Yezo scallop fall into two orders within the 9 to 950 µm range. For example, algae of the species *Chaetoceros affinis, Ditylum brightwelli, Dinophysis acuta* and *Protoceratium areolatum* measure 9-30 µm, 20-60, 60-70 and 25-28 µm respectively, while the animal species *Helicostomela longa, Penilia avirostris, Oithona similis* and mollusk larvae measure 40-63 µm, 200-950, 300-900 and 100-450 µm respectively. According to Broom's data (Broom, 1976), the size of food particles preferred by the scallop is 50-60 µm. It has been found that such size-different organisms as *C. affinis* or *P. avirostris* play the same role in the diet of the scallop.

A significant portion of the food organisms passes through the digestive tract of the scallop in an intact form. Apparently, the digestive organs are not capable of effectively digesting all the food, especially during abundant feeding (Reid, 1968). Only very minute particles and dissolved organic substances are captured by the cells of the digestive diverticula (Owen, 1974). It is believed that the externally intact food organisms secrete a large amount of soluble metabolites into the intestine of the mollusks, which has, for example, been noted for algae (Khailov, 1971; Jorgensen, 1975). It may be that these substances fill a significant part of the food requirements of the scallop (Tsikhon-Lukanina, 1976).

7.2. Intensity of grazing

The quantitative feeding characteristic of the Yezo scallop, which is expressed in average monthly values of the index of fullness, is depicted in Fig. 31. All of the specimens analyzed grazed during the summer—autumn period (from May to October); the index of fullness varied from 15.5 to 275.2%. In the majority of cases, the index of fullness in young one-year-old and two-year-old scallops was almost twice as high as in more mature specimens.

During the first half of May, a 5—9-year-old scallop in Starka Strait and Alekseyev Bay was at the pre-spawning stage. All of the scallops were in the process of grazing, the index of fullness in both areas ranging from 27.1 to 69.2%$_{00}$ and from 41.3 to 60.9%$_{00}$ respectively. During the spawning period, the intensity of grazing was lower (index of fullness 23.1-108.4%$_{00}$ in Starka Strait and 15.5-101.1%$_{00}$ in Alekseyev Bay).

In July, the intensity of grazing of a one-year-old scallop from suspended cages in Alekseyev Bay was very high (index of fullness 93.1-214.1%$_{00}$, an average of 149.5%$_{00}$).

In September and October, the intensity of grazing of these animals decreased somewhat (index of fullness 103.1 and 95.3%$_{00}$ respectively).

A photoperiodicity in relation to the intensity of grazing was noted in young scallops with a 4.3-5.5 cm shell, reared in suspended cages. In scallops caught at 5 o'clock in the morning (grazing at night), the index of fullness was twice as high (138.3-275.2%$_{00}$, average 178.6%$_{00}$) as in scallops caught during the day (59.9-112.4%$_{00}$, average 88.8%$_{00}$). Similar data were presented by

Yamamoto who showed that the rate of filtration in a scallop with a 4.2-6.6 cm shell increases significantly during the night (from 24.00 to 05.00 hours), when the most effective absorption of food takes place.

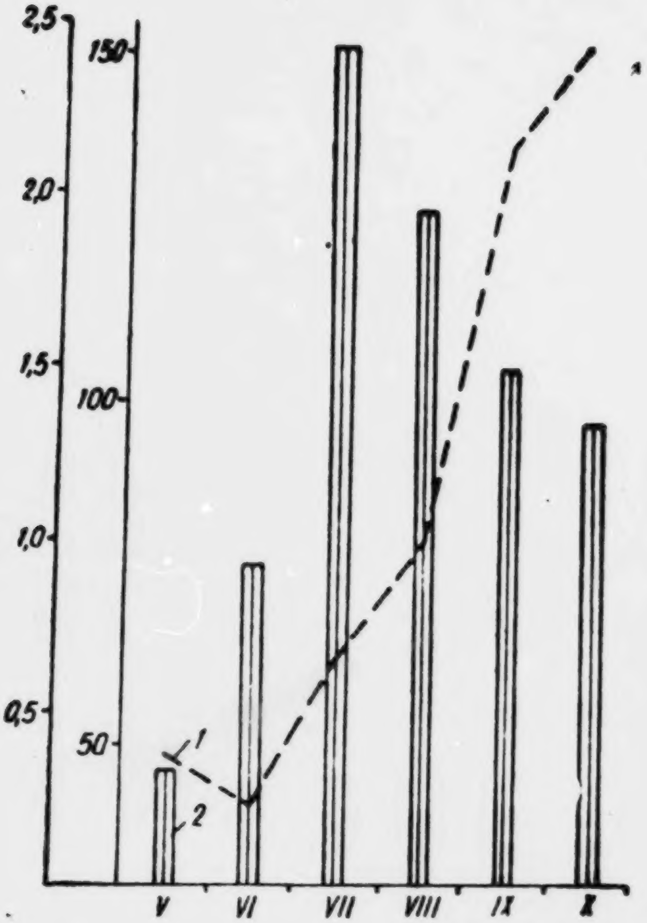


Fig. 31. Average monthly index of fullness of the digestive tract in the Yezo scallop and the plankton biomass in 1978. X-axis - months; Y-axis (left to right): 1 - plankton biomass, g/m^3; 2 - index of fullness, ‰o

The intensity of grazing of one-year-old scallops raised in suspended cages in Alekseyev Bay was compared with that of one-year-olds from the bottom of the same bay. The index of fullness of the scallops from the suspended cages was 1.5 times higher than in those living on the bottom (144.9 and 101.2‰ respectively). This is consistent with the data of some researchers who have shown that scallops living on artificial substrates have higher ecological-physiological potentials (Reznichenko, Soldatova, 1976). Judging by the average monthly index of fullness of the digestive organs, the scallop feeds most actively in June and August. In autumn, the intensity of grazing decreases, despite the increase in plankton biomass.

7.3. Selectiveness of grazing

Many researchers believe that the most intensive grazing of filter-feeding bivalves takes place during spurts in phytoplankton development. In the coastal waters of Peter the Great Gulf, three such spurts are usually observed, a spring spurt in March—April, a summer one in July, and an autumn one in October—November (Mikulich, Biryulina, 1977). In 1978, however, blooming of the phytoplankton began from the end of August due to the hydrologic conditions, and the summer spurt combined with the autumn spurt; as a result of this, zooplankton species prevailed in the coastal waters in June—July. Nevertheless, the intensity of grazing of the Yezo scallop in summer reached its maximum values (Fig. 31) mainly because of its feeding on detritus and animal organisms. The June diet of the scallop inhabiting Starka Strait consisted mainly of infusorians *H. longa* and *H. subulata* , and the crustacean *Evadne nordmani* , which were quite abundant in the plankton. Other species of bell animalcules were encountered singly in the food of the scallop and in the plankton. In July and August, the digestive tract of both cage-reared scallops and those from the bottom in the western part of Popov Is. contained an abundance of *H. longa, H. subulata* and especially the thermophilous water flea *Penilia avirostris* , the numbers of which increased significantly in the coastal plankton during this period. The same can be said about the small thermophilous crustacean *Oithona brevicornis* which was present in the food of the scallops cultivated in cages in July and in August, and was one of the main components of the zooplankton during the same months (its density reached 24,000 specimens/m^3 in August). As a prolific year-round species of the plankton, *O. similis* was encountered in the digestive tract of the scallop in July, August, September and October. In May and September, the diet of the Yezo scallop included large quantities of bivalve larvae which were particularly abundant in the plankton as well during these months (Mikulich, Biryulina, 1977).

In scallops reared in cages and in those living on the bottom, the digestive organs contained an abundance of diatomaceous algae of the species *Thalassiothris frauenfeldi* and *Ditylum brightwelli* , as well as various species of *Chaetocaros* among which *C. affinis* prevailed from August to October. All of these species also predominated in the plankton during this period. *Skeletonema costatum* was also consumed in large quantities by the scallop in September and October, and *Rhizosolenia alata* in October, which is when these species develop at the fastest rate. It has been noted that the composition of algae in the scallop's diet corresponds to their composition in the plankton. At first glance, *Protoceratium areolatum* and *Dinophysis acuta* appear to be an exception; they are consumed in abundance by the scallop in May and June, but are scarce or absent altogether in the plankton samples. This is due to the fact that, being very small, the peridinians freely pass through the mesh of a plankton net.

A comparison of the composition of the scallop's diet with the composition of the plankton shows that this mollusk unselectively filters all the different unicellular algae, comparatively small animals and detritus found in the water. This is confirmed by the contents of its digestive tract, which include inedible objects such as scales of butterfly wings, spores of coniferous plants, fragments of multicellular algae and fragments of eelgrass, all in proportion to their content in the plankton.

The presence of benthic organisms such as small amphipods and isopods, as well as algae of the genera *Navicula, Pleurosigma, Cocconeis* and *Nitzschia* in the scallop's diet indicates that the scallop gets its food not only from the suspension, but also from the thin near-bottom layer of water.

The data on the composition of the food consumed by the Pectinidae (Blegvad, 1915; Hunt, 1925; Bazikalova, 1930; McGinitie, 1941; Turpayeva, 1953; Kuznetsov et al., 1966; Zhyubikas, 1969; Reid, 1968; Broom, 1976) indicate that detritus is the basic food of the scallop in 58% of the cases, a secondary food in 25% of the cases, and not on record in 17% of the cases; the content of unicellular algae varies from 8 to 67%. The majority of authors regards animal organisms as a secondary food for the scallop, though animal organisms constitute the basis of the scallop's diet during certain periods. Only Hunt places animal organisms on a par with unicellular algae as the basic food of the scallop (Hunt, 1925). The variance in the data on the predominance of this or that food in the diet of the scallop is probably due to the fact that food composition was studied at different times of the year and in different water areas. If the composition of the scallop's diet were to be examined in accordance with the habitat and season, we would find that animal organisms and plants comprise a significant part of the scallop's diet during the periods of their mass development, and detritus is its basic food during the rest of the year.

Seasonal variations in food composition are noted in numerous species of marine and freshwater mollusks (Yablonskaya, 1967; Reid, 1971; Trevallion, 1971; Aliyev, 1975). This phenomenon is usually associated with the "blooming" of algae, and less commonly with the period of mass reproduction of invertebrates, especially protozoans. In temperate and cold waters, the instability of trophic sources is particularly well-defined; the flexibility of the scallop's diet in these waters is correspondingly high (Zernov, 1949).

According to Turpayeva's classification (1953), the scallop belongs to the filter-feeders of the 1st subgroup A (deposit-feeders) which get their food from the thin near-bottom layer of water; this subgroup is characterized by the absence of plankton in the digestive tract. In reality, however, plankton can form the basis of the scallop's diet. On suspended cages, the scallop feeds from the water, similar to the filter-feeders of the 2nd subgroup B (active filter-feeders).

Therefore, like other bivalves (Mironov, 1948; Romanova, 1963; Stasek, 1965; Mitropolsky, 1966; Reid, 1971; Theisen, 1972; Tsikhon-Lukanina, 1976), the scallop feeds on both benthic and planktonic organisms.

7.4. Grazing rate

The grazing rate can be judged by the quantity of food particles filtered by an individual from a given volume of water over a certain period of time and passed through the digestive tract. This value, expressed in units of mass or energy, is the physiological ration (Alimov, 1969), by means of which the food requirements of the scallop are met. We get a good idea of the quantity of food that is consumed by the scallop by determining the rate of filtration or the volume of water passed through the water-moving apparatus by one individual over a given period of time. The ration is equal to the rate of filtration multiplied by the concentration of suspension in the water. Since bivalves capture all or nearly all of the suspended particles (92-100% according to Kondratyeva, 1970), the rate of filtration (**F**) can be determined by the change in the concentration of suspension in accordance with Gauld's equation (Gauld, 1951), $\mathbf{F=v/n[(\ln C_0-\ln C_t)/t-a]}$, where $\mathbf{C_0}$ and $\mathbf{C_t}$ denote the concentration of suspension at the beginning and at the end of the experiment, **v** the volume of water, **t** the length of the experiment, and **n** the number of animals in the experiment. The value **a** is determined by the change in the concentration of suspension in the control tanks without animals during the same period of time, i.e. $\mathbf{a=\ln C_0-\ln C_t/t}$.

The process of water filtration by the scallop is a continuous one, but it can vary in its intensity. As we know (Yamamoto, 1964), the most active grazing in the scallop is observed at night (Fig. 32).

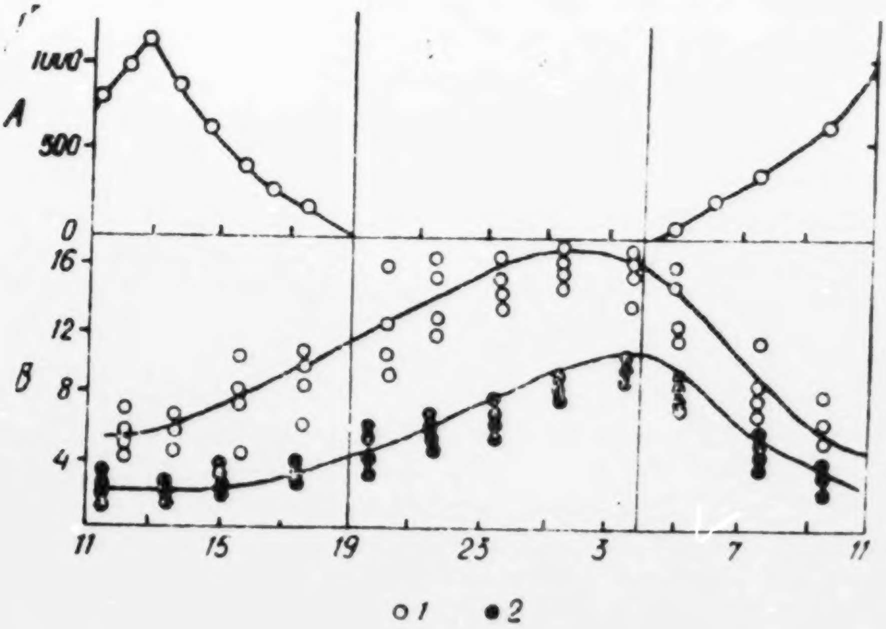


Fig. 32. Diurnal variability of the intensity of filtration in two size groups of the Yezo scallop (after Yamamoto, 1964): 1 - height of shell 10-25 mm, 2 - height of shell 42-66 mm. X-axis - time of day, h; Y-axis: A - intensity of light, lux; B - rate of filtration, ml/h/g fresh body wt.

When the intensity of illumination is at its maximum at midday (about 1000 lux), feeding activity is at its lowest, after which it begins to increase slowly. The same diurnal rhythm is observed in the mussel *Mytilus galloprovincialis* and the oyster *Crassostrea virginica* (Arakawa et al., 1971). Filtration increases after brief exposure of the mollusks to air and with a certain increase in the concentration of food particles.

The rate of filtration is greatly affected by water salinity. The rate of filtration decreases with gradual freshening of the water; for example, with a water salinity of 7-10‰, it is 15 times lower than normal (Makarova, 1979).

The rate of water filtration by the scallop at 10°C depends on the size of the mollusks, i.e. live body weight (W, g) and shell height (h, mm): $F=(0.366\pm0.03)W^{0'7\pm0'04}$ l/h/specimens;
$F=(0.52\pm0.03)10^{-3}h^{2'18\pm0'08}$ l/h/specimens.

For more accurate estimates, it is better to use the equation of dependence of the rate of filtration on the mass of the scallop.

The operation of the water-moving apparatus is greatly affected by temperature (Fig. 33). With an increase in temperature, the intensity of filtration increases rapidly, e.g. in a one-year-old scallop, it amounts to 0.096 l/h/g at 5°C, and increases more than 3-fold at 20°C. According to our data, the average value of the temperature coefficient Q_{10} in the 5—20°C interval is 2.53. To reduce the intensity of filtration of the Yezo scallop at any temperature to 20°C and vice versa, the estimated temperature corrections can be used (table 4).

Table 4. Temperature corrections (q) for reducing the intensity of filtration in the Yezo scallop to 20°C at Q_{10} average=2.53

t	q	t	q	t	q	t	q
5	4.02	9	2.78	13	1.91	17	1.32
6	3.67	10	2.53	14	1.74	18	1.20
7	3.34	11	2.31	15	1.59	19	1.10
8	3.05	12	2.10	16	1.45	20	1.00

The rate of water filtration is also affected by the concentration of suspended food particles or suspended organic matter (SOM). For example, our observations have shown that three-year-old scallops with a shell height of 100-105 mm filter 8.66, 8.94, 5.6 and 3.28 l/h/specimen with an SOM content of 1.04, 2.44, 3.13 and 4.88 cal/l respectively (12°C). The average annual concentration of suspended organic matter in Alekseyev Bay is equal to 1.42 cal/l. With SOM concentrations approximating natural ones, the filtration of water by the water-moving apparatus of the mollusks is at its highest. When the concentration of the suspension of food particles is increased 2.2- and 3.4-fold in relation to the average annual one, the intensity of filtration decreases 1.5- and 2.9-fold respectively (Fig. 34). This occurs because the water-moving apparatus of the mollusk becomes obstructed, the functioning of the adductor becomes arrhythmic, and the siphonal openings contract (Kondratyev, 1967). With very high concentrations of suspension, the filtering apparatus clogs up.

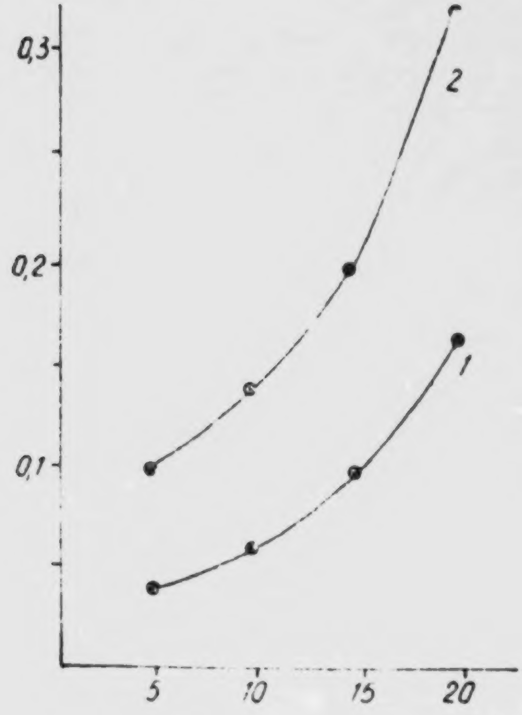


Fig. 33. Dependence of the rate of filtration on temperature in the Yezo scallop: 1 - fourth-year scallops, 2 - yearlings. X-axis - water temperature, °C; Y-axis - rate of water filtration, l/h/g of live body weight

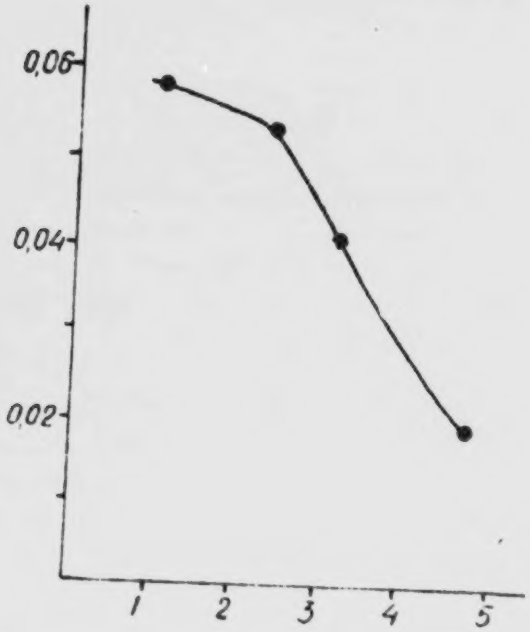


Fig. 34. Dependence of the rate of filtration on food concentration in the Yezo scallop at 12°C. X- axis - concentration of food, cal/l; Y-axis - rate of filtration, l/h/g of live body weight

Since the rate of filtration is determined by the quantity of filtered water and its content of suspended food particles when all other conditions are equal, the quantity of the rations naturally depend on these factors (body weight, temperature, the concentratiion of SOM) as well. For example, with an increase in the size of the mollusk and the temperature, the rations increase (table 5). The amount of food consumed also increases with the content of food particles in the water, but not more than two-fold as compared with the average annual value. A further increase in food concentration does not affect the ration, but it does increase its unassimilated part and the formation of pseudofeces (table 6). An increase in the quantity of pseudofeces excreted with an increase in the concentration of suspension has been noted for a number of bivalve species by numerous researchers (Tenore, Dunstan, 1973; Foster-Smith, 1975; Sanina, 1976). The ration at an initial concentration of suspension equal to 2.44 cal/l is the physiological ration; its value remains constant with a further increase in the concentration of suspension. The ecological ration of the mollusks and the quantity of unassimilated food is directly dependent on the concentration of suspension in the medium (Alimov, 1981).

The time it takes for swallowed food particles (microalgae *Pavlova lutheri, Phaeodactelym tricornutum* , yeast) to pass through the digestive tract at 17°C amounts to 80±5 and 93±10 min in mollusks with a shell height of 14-20 and 60-70 mm respectively. The intestine is filled 18 and 16 times a day (Makarova, 1982). The assimilability of food in the scallop is high, and does not depend much on the time of year; in young scallops more than a year old, it averages 80%, and with time decreases to 65-67% (Fuji, Hashizume, 1974).

Table 5. Ration (cal/specimen/day) of the Yezo scallop for different body sizes and water temperatures

Shell height, mm	Mass, g	Ration at 5°C	Ration at 10°C
60.7±2.1	27.6±1.8	86.86±25.67	113.78±17.51
122.5±1.2	253.3±8.7	373.43±69.87	473.53±142.87

Shell height, mm	Mass, g	Ration at 15°C	Ration at 20°C
60.7±2.1	27.6±1.8	196.70±17.80	234.87±16.24
122.5±1.2	253.3±8.7	875.29±41.32	1347.63±101.94

Table 6. Dependence of the ration and its unassimilable part (cal/specimens/day) on the concentration of food particles (cal/l) in the Yezo scallop

Concentration	Ration	Unassimilable part	Presence of pseudofeces
1.04±0.3	121.08±31.34	23.14±8.49	-
2.44±0.12	288.98±21.08	49.56±9.1	-
3.13±0.26	286.98±20.82	77.14±14.2	+
4.88±0.68	289.88±31.11	82.96±7.43	+

7.5. Age and seasonal variability of food consumption

Food consumption in the Yezo scallop has not been researched very well. There has been only one attempt (Fuji, Hashizume, 1974), under conditions closest to natural ones, to calculate the so-called ecological rations which consist of the food that finds its way into the digestive tract and the particles rejected as pseudofeces. The ration was determined for scallops of three age groups (initial shell height 5.06 cm, 9.63 cm and 11.55 cm respectively) six times in one year as the sum of the energy equivalents of body increments, and the losses on respiration and excreted biodeposits consisting of feces and pseudofeces. After analyzing the material of these authors and assuming that feces comprise an average 70% of the biodeposits of the scallop (Tsuchiva, 1981), we managed to calculate the physiological rations (table 7).

Table 7. Dynamics of food consumption in scallops of different age (after Fuji, Hashizume, 1974)

Time period	No. of days	Water temp. °C	Average body mass, g	Ration		
				ecological	physiological	
				kcal/spec.	kcal/spec.	% of body mass/day
			First-year			
Aug.-Oct.	72	22.8-14.3	9.75	7.0	6.1	0.87
Oct.-Dec.	58	14.3-5.5	13.44	12.0	10.26	1.30
Dec.-Feb.	62	5.5-4.2	21.12	16.0	14.10	1.11
Feb.-Apr.	61	4.2-9.2	29.24	22.0	19.9	1.11
Apr.-June	60	9.2-17.4	36.56	20.0	18.0	0.82
June-Aug.	62	17.4-22.8	46.45	31.0	29.0	1.00
			Second-year			
Aug.-Oct.	72	22.8-14.3	46.73	27.5	26.0	0.77
Oct.-Dec.	58	14,3-5.5	45.66	20.0	17.0	0.64
Dec.-Feb.	62	5.5-4.2	57.80	46.0	42.5	1.20
Feb.-Apr.	61	4.2-9.2	75.76	61.0	54.0	1.17
Apr.-June	60	9.2-17.4	85.28	45.0	41.6	0.81
June-Aug.	62	17.4-22.8	88.05	34.0	34.2	0.62

(table 7 continued)

Time period	No. of days	Water temp. °C	Average body mass, g	Ration		
				ecological kcal/spec.	physiological	
					kcal/spec.	% of body mass/day
			Third-year			
Aug.-Oct.	72	22.8-14.3	76.55	34.0	38.8	0.70
Oct.-Dec.	58	14.3-5.5	73.10	27.5	23.3	0.55
Dec.-Feb.	62	5.5-4.2	90.37	66.3	58.9	1.05
Feb.-Apr.	61	4.2-9.2	110.17	68.0	67.8	1.00
Apr.-June	60	9.2-17.4	118.46	66.5	53.7	0.76
June-Aug.	62	17.4-22.8	119.21	41.5	50.1	0.68

As seen in table 7, the absolute rations increase rapidly and constantly throughout the first year as the immature scallop grows. In mature scallops, they are high during the period of active maturation of the gonads (December—February), and reach their maximum values in the pre-spawning period (February—April). Food consumption then decreases over the following four months. The values of the relative rations change in a similar manner, i.e. with a significantly smaller amplitude of fluctuations, they are the highest from December to April in all the age groups of the scallop. Such a high rate of grazing is apparently due to the higher than usual metabolic activity of the mature individuals during the reproductive period.

7.6. Production of biodeposits

The interest in determining the volume of the biodeposits produced by the scallop is spurred primarily by the demands of mariculture; these mollusks are active filter-feeders, and the precipitable suspension of their feces and pseudofeces can cause contamination and degradation of the pelagic and benthic biocoenoses in the case of high-volume mariculture.

The age and seasonal production of biodeposits has been researched by Fuji and Hashizume (1974). According to their data, the quantity of biodeposits is directly dependent on the intensity of grazing (table 8). Body size also affects the production of biodeposits, but not to the same extent. According to Tsuchiva (1981), the absolute quantity of precipitable feces (X) and pseudofeces (Y) increases and the relative quantity decreases as the body mass (W) of the scallop increases. The production of biodeposits depends very little on water temperature, and reaches its maximum value in the 3-13°C range; however, it decreases at 20°C and higher (table 9). The relationship between W and X, and between W and Y is of a parabolic nature.

Table 8. Production of biodeposits (kcal/specimen) by scallops cultivated in suspended cages (after Fuji, Hashizume, 1974)

Time period	First-year	Second-year	Third-year
Aug.-Oct.	1.52	10.62	13.6
Oct.-Dec.	1.59	8.23	10.0
Dec.-Feb.	3.53	14.14	15.54
Feb.-Apr.	5.83	28.25	26.50
Apr.-June	5.13	14.21	18.42
June-Aug.	4.37	5.06	13.44

Knowing the size composition of the scallop under suspended culture in Mutsu Bay, the linear body size and body weight relations, as well as the relationships presented in table 9, Tsuchiva was able to calculate the production of biodeposits by the scallop of this bay. It was found that, in October 1980, at a temperature close to 20°C, $8.31 \cdot 10^8$ underyearlings produced 5.39 tons of feces and 1.6 tons of pseudofeces in one day, and $2.08 \cdot 10^8$ year-old scallops deposited 2.97 and 1.53 tons respectively. The author notes that the production of pseudofeces in the Yezo scallop increases per unit of time with the concentration of food, while the production of feces remains unchanged. This indicates that the scallop consumes only the required amount of food, equal to the physiological ration, and excretes the rest as pseudofeces.

Table 9. Dependence of biodeposition on the body mass of the scallop and water temperature (after Tsuchiva, 1981)

Feces

Temperature, °C	mg/spec./day			mg/g/day		
	a	c	r	a_1	c_1	r_1
3-6	3.30	0.451	0.684	3.29	-0.548	-0.755
10-13	1.37	0.662	0.740	1.329	-0.323	-0.470
20-22	5.14	0.250	0.423	5.77	-0.769	-0.834
25	0.368	0.79	0.849	0.343	-0.20	-0.39

Pseudofeces

Temperature, °C	mg/spec./day			mg/g/day		
	b	d	r	b_1	d_1	r_1
3-6	0.634	0.605	0.823	0.692	-0.428	-0.710
10-13	0.506	0.616	0.758	0.609	-0.431	-0.689
20-22	1.335	0.386	0.485	1.692	-0.664	-0.676
25	0.133	0.860	0.853	0.127	-0.130	-0.247

Note: r, r_1 - coefficients of correlation

8. RESPIRATION

The respiratory process in the Yezo scallop consists in the pumping of water through the mantle cavity where dissolved oxygen is extracted by the gills. The rate of respiration, or metabolism (the amount of oxygen consumed by the animal per unit of time), and its intensity (the rate associated with body mass), though they do depend on numerous factors (body size, maturity of the gonads, water temperature), give us the same picture of metabolic activity for the given conditions.

An exponential relation of the type $Q=A \cdot W^b$, where A and b are coefficients (common for the most diverse organisms), is observed between the rate of metabolism (Q) and body mass (W), or mass of the soft tissues, in the scallop. The first coefficient corresponds to the value of metabolism in an animal with a mass equal to 1, and the second coefficient corresponds to the rate of metabolic change as the mass of the animal increases.

The equations of dependence of the oxygen consumption rate on dry tissue mass at different times of the year (table 10) show that the values of the exponential constant differ from their mean value (0.80) by not more than 8%, and approximate 0.75 which is the most characteristic value for numerous poikilothermic and homoiothermic animals (Hemmingsen, 1960). The level of metabolism (A) is distinguished by a much higher degree of variability.

According to our data, the dependence of the rate of metabolism on live body mass at 20°C in the Yezo scallop is expressed by the formula $Q=0.163\pm0.011W^{0'74\pm0'03}$ mg/spec./h (20°C), where W is expressed in grams. The dry mass of the tissues averages 4.7% of the live body mass of the scallop. Tsuchiva gives unusually low and, apparently, incorrect values of the exponential constant (0.422-0.487) in the equations of dependence of metabolism on body mass for the Yezo scallop (Tsuchiva, 1981).

The effect of reproductive activity on energy metabolism in the Yezo scallop is illustrated in table 11. At the stage of active gametogenesis, despite the 0° temperature of the water, the intensity of oxygen consumption was only half of what it was in July at 18°, and 1.5 times lower than in October at 9°. At 5°C in March and April, the intensity of metabolism at the prespawning stage of gonadal maturity was the same as at 18°C at the stage of relative rest. At the spawning stage, despite an increase in temperature to 8°C, the intensity of metabolism again decreased, reaching the level of early gametogenesis. Consequently, there is no doubt that the level of gametogenesis does have a significant effect on energy metabolism in the Yezo scallop. If this type of effect were associated with water temperature alone, then the intensity of oxygen consumption in April, for example, would be 3.4 times lower than in July. An increase in metabolism at a lower than usual temperature, due to reproductive activity, has been noted in many bivalve mollusks (Dam, 1954; Vooys, 1976; Vahl, 1978). A diurnal rhythm of respiration is not noted in the Yezo scallop.

Table 10. Dependence of the rate of metabolism on the dry mass (W, g) of the soft tissues (A, mg/h) in the Yezo scallop

Period	Water temp. °C	Mass range	A	b	Ref.
Aug.	20-22.8	0.85-18.9	0.828	0.817	Fuji, Hashizume, 1974
Oct.	14.3-15.2	0.85-18.9	0.569	0.777	"
Dec.	5.5-6.2	0.85-18.9	0.263	0.862	"
Feb.	4.2-5.0	0.85-18.9	0.292	0.796	"
Apr.	8.6-9.2	0.85-18.9	0.419	0.822	"
June	16.4-17.4	0.85-18.9	0.665	0.763	"
Apr.-June	11-20	0.037-18.3	0.900*	0.76	Bregman et al., 1977
July-Aug.	20	0.0011-18.3	1.39	0.74	Our data

*Adjusted to 20°C along the "normal curve" (Vinberg, 1968).

The intensity of metabolism of the scallop as a poikilothermic organism greatly depends on temperature (table 12). Prior to determining metabolism, the mollusks were acclimatized for 3-15 days. Depending on the initial water temperature, exposure time was 3-6 hours. The mean value of Q_{10}, which amounted to 2.63 in the 5-20°C range, was calculated on the basis of experimental data. For comparison, we can say that this value approximates the one for *Chlamys opercularis* (McLusky, 1973).

Zhakin (1979) gives the following Q_{10} coefficients for the Yezo scallop:

t°C	0—5	5—10	10—15	15—20	20—25
Q_{10}	4.36	2.75	1.18	0.99	0.92

Such a significant discrepancy in coefficients is probably due to insufficient acclimatization (scallops acclimatized from 9 to 17°C in only one day) and the different physiological state of the mollusks; the experiments were carried out in October (10°), January (-1.8°), April (4.0, 7.5, 9.0°) and July (25°) in the sea and in a laboratory. All the other experiments were carried out in July—September at the stage of relative rest of the sexually mature scallop. At the same time, the Q_{10} values calculated on the basis of our own material were in the range of 2—3 which is common for all animals (Ivleva, 1981).

Table 11. Intensity of metabolism in the Yezo scallop at different stages of gametogenesis

Stage of gametogenesis	Live body mass, g	Raw mass of tissues, g	Raw mass of gonads, g	Gonadal index	Intensity of metabolism, mg/h/g live wt
Relative rest	193.5±19.8	56.5±5.6	3.3±0.6	5.84	0.031±0.002
Onset of development	176.1±3.8	58.2±1.4	5.7±0.9	9.79	0.021±0.002
Active gametogenesis	207.7±11.2	81.9±6.3	9.4±1.4	11.48	0.150±0.001
Prespawning	155.8±12.8	54±4.9	10.3±1.4	19.07	0,030±0.002
Spawning	154.7±18.6	43.4±7.2	8.8±2.1	20.28	0.020±0.0020

Note: Our own and G.I. Viktorovskaya's data are used in the table.

Table 12. Energy metabolism of the Yezo scallop under different temperature conditions

Shell height, mm	Mass, g	Rate of metabolism (mg/hr/specimen) at			
		5°C	10°C	15°C	20°C
7.7±0.1	0.048±0.002	0.0019	0.0032	0.0053	0.0075
42.8±1.1	10.3±0.7	0.34±0.05	0.34±0.05	0.15±0.05	0.86±0.04
122.7±4.4	213.8±22.4	1.86±0.24	2.09±0.35	3.45±0.71	6.02±0.11

The material examined in this section gives us an idea of the quantitative dependence of the rate of metabolism on the mass of the body and tissues of the Yezo scallop, the physiological state of the mollusks and water temperature, and confirms the exponential nature of the dependence of the oxygen consumption rate on the mass of the metabolically active parts of the body. At the same time, the condition of the mollusk itself, as well as the nature and level of the environmental factors, undergo constant change in a natural environment, and their effect on the processes of metabolism is ambiguous. Consequently, it is impossible to describe the dependence of metabolism on body mass for the entire year by a single equation. It would inevitably have to include such factors as water temperature, the quantitative index of gonadal maturity (more precise than the gonadal index), the partial pressure of the oxygen dissolved in the water, the degree of illumination, and the flow velocity of the water. The latter three definitely affect the life activity of the scallop.

Therefore, future investigations of the metabolic processes in the Yezo scallop should be aimed at developing objective quantitative criteria for the physiological state of the mollusk, and at determining the effect of the above-mentioned factors.

9. BIOCHEMICAL COMPOSITION

9.1. General biochemical composition

Table 13 gives the total chemical composition of the principal components of a number of organs of the Yezo scallop (Kizevetter, 1973). A high content of free amino acids (from 140 to 1950 mg%) is found in the muscle which is the main nutritional part of the scallop. Nonprotein nitrogenous substances constitute 350-720 mg%. The nitrogenous bases (mainly trimethylamine oxides), which determine the palatability and aroma of the meat, constitutes from 1 to 580 mg%. A wide range is also observed in the vitamin content of the muscle (B_1 - 0.06-0.7 mg%, B_2 - 0.01-0.29 mg%, B_{12} - 50-250 μg/kg, C - 8 mg%). The content of ascorbic acid in the mantle fluctuates from 5 to 17 mg% (Kizevetter, 1973). Five carotinoids have been identified in the gonads of the sea scallop; they are pectenolone, pectenoxanthin, diatoxanthin, astaxanthin, and 3,4,3'-trioxy-7',8'-dihydro-β-carotene (Matsuno et al., 1981). Hormones were found in the organs and tissues of the Yezo scallop. According to Nikitina (1982), large quantities of glucocorticoids are present in the cardiac muscle, their content being higher in the females (8.5 μg/g) than in the males (6.176 μg/g). A large concentration of this hormone was found in the foot muscle (3.3-8.2 μg/g), gills (1.8-2.6 μg/g) and stomach wall (1.59-2.07 μg/g). The content of hydrocortisone amounts to 0.375-1.233 μg/g in the gonads, and about 0.3 μg/g in the mantle and kidneys. The lowest content of hydrocortisone (0.047 μg/g) and corticosterone (0.0779 μg/g) is noted in the adductor muscle. The presence of serotonin and catecholamines was established in the neurons of the ganglia of the Yezo scallop by histochemical methods (Varaksin et al., 1982). The same authors used spectrofluorimetric methods to show that serotonin was the predominant monoamine in the nervous system, especially in the cerebropleural and pedal ganglia. A higher content of serotonin in comparison with dophamine is also noted in the gonad (7.7 and 0.45 µg/g respectively.

The highest content of lipids is found in the ovaries. On the other hand, proteins and glycogen prevail in the muscles.

Table 13. Biochemical composition of organs in the Yezo scallop (%)

Organ	Water	Lipids	Protein	Glycogen	Minerals
Muscle	74.7-76.9	0.5-0.9	17.8-19.1	2.0-3.4	1.3-2.0
Mantle	83.8-87,0	0.7-1.2	9.8-12.8	0.8-1.2	2.3-2.9
Ovaries	80.6-89.3	0.9-2.4	6.9-8.4	-	1.9-3.0

9.2. Proteins

The proteins of the muscle tissue of the mollusk have been studied to the greatest extent. The protein composition of the myofibrils of the obturator muscles has been established (Margulis, Pinayev, 1977; Sheludko et al., 1978). Actin and myosin prevail in quantity. The minor contraction proteins consist of α-actine and paramyosin. Troponins and the light chains of myosin are absent, but proteins with a molecular mass of 16,000, 29,200 and 48,000, characteristic of the Yezo scallop, are noted. The complex subunitary structure of myosin was shown with the help of electrophoresis in polyacrylamid gel with urea (Kondo, Morita, 1981). In addition to the contraction proteins, Ca^{2+}-dependent protein (calmodulin) was isolated from the muscle of the scallop. This protein is a modulator of many Ca^{2+}-dependent enzymes, including adenylate cyclase, membranous ATP-ases, phosphorylkinase and phosphodiesterase. The calmodulin of the scallop differs from that of vertebrates in a number of properties (Iazawa et al., 1980). In the scallop, it contains 148' amino acids in a polypeptide chain, and it has a molecular mass of 16,720. A molecule of protein contains one N-trimethyllysine group and one histidine group, as well as a large number of acidic amino acids, but there is no tryptophan or cysteine. Mollusk calmodulin contains one tyrosine group, whereas the same protein in vertebrates contains two. When comparing the amino acid composition of scallop and vertebrate calmodulins, Toda et al. (1981) noted three amino acid substitutions, in position 99 (tyrosine—phenylalanine), position 143 (glycine—threonine) and position 147 (alanine—serine).

The cytoplasmic proteins in the organs of the Yezo scallop have been studied to a smaller extent. It has been found that the cytoplasm in the cells of the digestive gland contains proteins that can tolerate lecithin from the liposomes in the mitochondrial membrane to the same extent as the analogous proteins in the liver of rats (table 14). The cytoplasmic lipid-exchanging proteins are not species specific to the acceptor membranes, i.e. the exchange of phosphatidylcholine molecules is equal to that in "foreign" mitochondria (systems C and D). The capacity of these cytoplasmic proteins to tolerate alkenylacyl (plasmalogenic) and diacyl forms of phospholipids was also examined. As seen in table 15, the transport of both forms of phosphatidylcholine was equally stimulated by both the lipid-exchanging proteins of the rat liver, and by the analogous fraction of the digestive gland of the scallop. In addition to the lipid-tolerant proteins, specifically cadmium-binding proteins are found in the cytoplasm of the cells of the digestive gland and other organs of the Yezo scallop. The capacity to accumulate large quantities of cadmium in the digestive gland, even in clean waters, is a characteristic feature of the scallop (Brooks, Ramsby, 1965; Bryan, 1973; Khristoforova, 1982). Normally, most of the cadmium in the cells of the digestive gland of the scallop is bound to microsomes, but with an increase in the concentration of the metal in the medium, a part of the cadmium binds with the cytoplasmic proteins. Separation of these proteins in a G-75 Sephadex column gives us several protein fractions with a high concentration of cadmium in the region where proteins with a molecular mass of 13,000 come out. The content of cadmium in these proteins doubled at the end of the experiment. As we know, specific proteins with a molecular mass of 8000-15,000, called metallothioneines, are synthesized in the cytoplasm of cells in response to the uptake of certain quantities of cadmium, zinc, copper and a number of other metals (Webb, Cain, 1982). According to gel-chromatographic data, new proteins are not synthesized in the digestive gland of the Yezo scallop; the cadmium entering the organism is bound by the proteins already present in the cytoplasm, which apparently have the properties of metallothioneines. With a significant increase of cadmium in the water (0.5 mg/l), the excess quantities of the metal are bound by cytoplasmic proteins with a high molecular mass. During the experiment, the specific concentration of cadmium increased from 0.1 to 6-9 µg/mg of protein in the high-molecular proteins, and from 0.2 to 2-3 μg/mg of protein in the metallothioneine-like proteins.

Table 14. Transport of phosphatidylcholine (PC) from liposomes to mitochondria in the presence of Yezo scallop and rat cytoplasmic fractions.

Incubation system	Without a supernatant	With a supernatant
A	6.6±0.8	35.0±1.8
B	4.8±0.5	31.8±2.3
C	6.4±0.5	33.4±2.4
D	5.7±0.2	35.3±1.4

Note: A - mitochondria of mollusk—supernatant of mollusk—^{14}C-PC-liposomes;
B - mitochondria of rat—supernatant of rat—liposomes;
C - mitochondria of rat—supernatant of mollusk—liposomes;
D - mitochondria of mollusk—supernatant of rat—liposomes.
Degree of transport determined in % of ^{14}C-PC of total PC content of mitochondria.

Table 15. Transport of diacyl and alkenylacyl PC from liposomes to mitochondria in the presence of Yezo scallop and rat cytoplasmic fractions

Supernatant fraction	Diacyl PC		Alkenylacyl PC	
	passive	active	passive	active
Rat liver	4.9±0.8	22.2±1.8	5.8±0.7	18.8±1.9
Digestive gland of scallop	5.0±0.9	24.3±1.5	5.7±0.7	25.1±0.7

Note: Passive transport - transport of ^{14}C-PC without cytoplasmic proteins.
Active transport - transport of ^{14}C-PC with cytoplasmic proteins.
Degree of transport determined as in table 14.

9.3. Enzymes

The main portion of the digestive enzymes in the Yezo scallop is concentrated in the digestive gland, while the hydrolases that split the carbohydrate-containing biopolymers are concentrated in the crystalline style. The scallop's ration consists mainly of polysaccharides, the component parts and products of the life activity of algae; because of this, the crystalline style, the concentrator of enzymes, contains highly active cellulases, laminarinases and glycosidases. The specific activity of the laminarinases is equal to 4 units/mg of protein in the digestive gland of the scallop, and 13.2 units/mg of protein in the crystalline style (Sova et al., 1970).

Carboxymethyl cellulase activity is the decisive one both in the digestive gland, and in the crystalline style (Elyakova, 1972). Alginases are either absent in the soft tissues, or their activity is insignificant (Favorov, Vaskovsky, 1971). The digestive gland of the Yezo scallop has been found to contain various glycosidases, namely N-acetyl-β-D-glucosaminidases, N-acetyl-β-D-galactosaminidases, β-glucosidases, α-glucosidases, β-galactosidases, α-galactosidases, β-xyloxydasases, β-xyloxydases, α-xyloxydases, β-mannosidases, α-mannosidases, N-acetyl-α-D-glucosaminidases and carbogydrases (Molodtsov et al.,1974; Molodtsov, Vafina, 1974).

The protease and lipase activity in the scallop is insignificant. No proteolytic activity with substrates such as hemoglobin, casein and gelatin was detected (Kozlovskaya, Vaskovsky, 1970). A low level of activity was noted in phospholipases A (Vaskovsky, Suppes, 1972), the predominant one being phospholipase A_2 (Suppes et al., 1977). A high level of activity was noted in lysophospholipase in the digestive gland, and a low level in the gills; lysophospholipase activity was not noted in the crystalline style, mantle and muscle (Latyshev, Vaskovsky, 1977).

Enzymes of energy metabolism, i.e. $Mg^{2}+$—ATPase, as well as acidic and alkaline phosphatases (table 16), have been identified in the organs of the Yezo scallop. Na+, K+—ATPase is localized in the plasmic membranes, and its activity greatly depends on the ATP content in the medium (Verzhbinskaya, 1982). Table 17 contains data on the activity of the acidic and alkaline phosphatases in the organs of the scallop during the period of low metabolic activity (February-March). Phosphatase activity increases considerably during the prespawning period.

The content of steroid and triterpene glycosides in the organs of the Yezo scallop is unknown, but the activity of the glycosidases that hydrolyze these compounds has been determined in the digestive gland and the crystalline style (Elyakova et al., 1974). Furthermore, histochemical methods have helped to identify enzymes of sex horome synthesis in the gonads of the scallop, and choline acetyl transferase in the neurons (Varaksin et al., 1982).

Table 16. Activity of Mg^{2+}—ATPase in the organs of the Yezo scallop (µmole of inorganic P/g of fresh mass/h)

Organ	Total Mg^{2+}—ATPase	Insensitive to ouabain	Sensitive to ouabain
Mantle	27	20	7
Gills	25	17	8
Obturator muscle	30	23	7

Table 17. Phosphatase activity in the organs of the Yezo scallop

Organ	Alkaline phosphatase, µmole/min/mg protein	Acidic phosphatase, µg P/h/mg protein
Digestive gland	0.30±0.05	32.5±1.2
Gills	0.20±0.04	11.5±1.7
Mantle	0.14±0.01	7.0±1.3
Muscle	0.11±0.02	4.5±1.1
Testis	0.16±0.04	7.5±0.4
Ovary	0.14±0.07	6.7±0.8

9.4. Lipids

According to Kostetsky (1985), phospholipids comprise 34.7% of the total lipids in the soft tissues of the Yezo scallop. The content of phospholipids in the organs varies significantly, 12.1-17.3% in the digestive gland, 57.6-60.5% in the gills, 62.5-74.5% in the testis, and 25.0-28.5% in the ovaries. The composition of the individual phospholipid classes in the organs is shown in table 18. Most of the lipids in the cells of the digestive gland of the Yezo scallop are not associated with the membranes, and are found in the cytoplasm (table 19).

However, while the cytoplasmic lipids are mainly neutral lipids, the membrane lipids consist only of phospholipids and cholesterol. The membranes of the mitochondria have the highest content of phospholipids. The distribution of the individual phospholipid classes in the cell is shown in table 20.

Table 18. Phospholipid composition of the organs in the Yezo scallop (% of the total phospholipids)

Phospholipid class	Digestive gland	Gills	Ovaries	Testes
Phosphatidyl choline (PC)	41.8±0.3	39.0±0.5	42.2±0.6	43.9±0.6
Phosphatidyl ethanolamine (PE)	27.8±0.4	33.4±0.5	32.5±0.8	31.1±0.1
Phosphatidyl serine (PS)	6.1±0.4	7.9±0.8	4.5±0.1	5.4±0.2
Phosaphatidyl inosite (PI)	8.1±0.7	4.5±0.4	5.5±0.1	4.4±0.2
Cardiolipin	3.7±0.7	2.4±0.2	3.3±0.1	4.9±0.4
Ceramide aminoethylphosphonate$_1$ (CAEP)	6.9±0.1	7.5±0.2	5.9±0.2	7.7±0.2
Ceramide aminoethylphosphonate$_2$	3.2±1.2	5.0±0.3	4.9±0.1	2.6±0.1
Lysophosphatidyl choline (LPC)	3.3±0.8	Traces	1.1	-
Lysophosphatidyl ethanolamine (LPE)	Traces	-	-	-

Table 19. Lipid composition of the cell membranes and cytoplasm in the digestive gland of the Yezo scallop (% of the total lipid content)

Component	Nucleus	Plasmic membrane	Mitochondria	Microsomes	Cytoplasm
Lipids, mg/mg of protein	0.045	0.394	0.240	0.473	0.746
Phospholipids	49.6±1.3	56.9±1.0	80.0±1,2	68.1±1.1	2.2±0.5
Cholesterol	17.1±1.0	16.6±1.2	11.1±0.7	13.6±0.8	Traces
Triglycerides	Traces	Traces	Traces	Traces	34.1±0.7

As in the organelles of vertebrates, PC and PE are the main phospholipids in the membranes of scallops. The distinguishing feature of the scallop membranes is the presence of large quantities of phosphonic sphingolipid, ceramide aminoethylphosphonate (CAEP). Of all the cell organelles of the digestive gland, the mitochondria have the most clearly defined specificity in phospholipid composition, i.e. their content of CAEP and PS is low, but practically all the cardiolipin of the cells is localized in them. A high content of plasmalogens is found in the membranous structures, and a low content in the hyaloplasm. The lipids of the subcellular fractions of the mollusk contain the characteristic series of fatty acids. The level of unsaturated fatty acids is high both in the polar, and in the neutral lipid fractions of the organelles. Monoenic acids are responsible for this in the neutral fraction, whereas polyenic acids prevail in the polar lipids. The cytoplasmic lipids not associated with the membranes are characterized by a high degree of nonsaturation. The mitochondrial lipids are distinguished by a particularly high content of unsaturated acids, mainly polyenic ones (table 21). A lipid extract of the soft tissues of the Yezo scallop also contains glycolipids which make up 1.2% of all the lipids (Vaskovsky et al., 1970). Pentose-containing glycolipids and trace amounts of cerebrosides and glycolipids with an average polarity were detected by means of qualitative methods. The hydrolysates of glycolipid extracts were found to contain an abundance of galactose and glucose, an average quantity of arabinose, and absolutely no fucose, rhamnose or xylose. The muscles of the mollusks were found to contain homobetaine, which produces a hypocholesterinemic effect. Other betaines have also been isolated and quantitatively determined from the tissues of the Yezo scallop (Abe, Kaneda, 1975).

Fig. 20. Phospholipid composition of the cell membranes and cytoplasm in the digestive gland of the Yezo scallop (% of the total content of phospholipids)

Phospholipids	Nucleus	Plasmic membrane	Mitochondria	Microsomes	Cytoplasm
PC-diacyl	38.0±1.0	41.4±1.0	47.8±1.7	44.0±1.2	42.8±1.2
PC-plasmalogen	5.9	9.9	4.9	3.4	5.4
PE-diacyl	9.4±0.3	7.7±0.4	6.8±0.2	6.3±0.2	2.2
PE-plasmalogen	12.4	9.9	16.6	15.1	2.1
PS-diacyl	3.9±0.1	5.2±0.7	2.4±0.3	6.9±0.3	5.1
PS-plasmalogen	3.3	4.0	2.3	2.4	-
$CAEP_1$+$CAEP_2$	11.4±0.2	10.1±1.0	2.9±0.1	10.6±1.0	16.4±0.8
DPG	Traces	1.3±0.1	11.0±0.4	0.7±0.05	-
PI	6.0±0.3	6.5±0.5	5.3±0.3	6.4±0.05	12.4±1.0
LPC	5.4±0.5	1.8±0.1	Traces	2.2±0.3	13.6±1.0
LPE	4.1±0.1	2.2±0.1	Traces	1.5±0.3	-
Plasmalogens	21.6	23.7	23.8	20.8	8.5

Note: Our own and N.V. Zhukova's data are used in the table.

Table 21. Fatty acid composition of lipids in the cell membranes and cytyplasm of the digestive gland (% of total acid content)

Acids	Nucleus		Plasmic membrane		Mito-chondria		Microsomes		Cytoplasm	
	N	P	N	P	N	P	N	P	N	P
14:0	8.1	10.2	11.9	7.5	2.4	6.7	6.1	9.6	16.6	9.6
14:1	0.8	0.4	0.8	1.0	Traces	Traces	0.9	0.7	0.4	0.7
16:0	18.5	19.6	22.6	23.2	23.8	24.6	34.4	28.2	25.2	22.2
16:1	12.7	21.8	9.0	11.2	1.8	25.7	8.9	25.4	21.0	19.0
18:0	7.4	5.0	6.3	17.8	8.6	4.0	10.0	5.6	1.2	3.0
18:1	14.0	13.5	8.0	14.3	12.0	17.8	13.7	17.3	8.9	11.4
18:2	1.0	3.4	0.5	4.0	1.7	3.0	0.7	3.6	-	3.7
18:4	12.5	5.7	6.6	6.0	10.5	3.1	7.8	5.3	2.9	7.0
20:1	-	-	0.5	Traces	Traces	2.1	Traces	-	3.1	0.6
20:4ω6	16.8	-	13.6	-	7.1	-	4.5	-	4.4	-
20:5ω3	7.8	8.1	14.3	4.9	18.0	1.8	9.3	2.5	11.4	19.5
22:1	-	11.0	-	8.8	-	8.7	-	1.3	-	1.5
22:6ω3	Traces	-	4.1	-	14.0	Traces	3.0	-	3.2	-
Unsaturated	66.0	64.4	58.9	50.2	65.1	64.2	48.5	56.1	56.2	65.1
Polyenic	38.5	17.7	39.1	14.9	51.3	7.9	25.3	11.4	22.8	30.2

Note: N - neutral fraction, P - polar fraction

Table 22. Mineral composition of organs in the Yezo scallop (10^{-3}% dry wt.)

Organ	Ti	V	Cr	Mn	Fe	Co	Ni	Cu	Zn	Mo
Muscle	-	0.8	-	0.6	3.1	-	-	0.2	-	-
Mantle	-	Traces	-	0.3	1.2	-	0.4	0.6	7.8	0.5
Gills	0.6	-	0.7	4.4	2.4	0.3	1.6	5.5	39.0	0.7
Digestive gland	0.5	6.4	-	0.3	5.7	Traces	0.5	6.4	20.2	0.6
Gonad	-	-	-	0.4	6.0	-	0.7	20.2	-	1.1

9.5. Carbohydrates

According to Kizevetter (1973), the content of monosaccharides, disaccharides and polysaccharides in the muscle of bivalve mollusks constitutes 8-24% of the dry defatted substance, and 12-42% in the mantle. The content of glycogen, the main neutral component of crude polysaccharide compounds ranges from 8.5 to 19.7% in the muscle, and from 10.9 to 40.8% in the mantle. Glucosamines and uronic acids have been identified in the polysaccharide fraction of the soft tissues in the Yezo scallop (Ovodov et al., 1969).

9.6. Mineral composition

The mineral composition of the Yezo scallop has been poorly researched. Data on the concentrations of sodium and potassium in scallop muscles and gills are available (Verzhbinskaya, 1982). The distribution of polyvalent, specifically heavy, metals has been studied in greater detail (Belcheva et al., 1979; Yevtushenko, Lukyanova, 1982; Khristoforova, 1982). Belcheva and coauthors (1979) established the mineral composition of various organs in scallops from Vostok Bay of the Sea of Japan (table 22). The highest concentrations of cadmium were found in the digestive gland (142.8-410 µg/g), but they vary depending on the habitat of the scallop, its age, and the time at which it was caught (Khristoforova, 1982). The subcellular distribution of cadmium and zinc in the digestive gland of the scallop is given in table 23.

Table 23. Subcellular distribution of cadmium (numerator) and zince (denominator) in the digestive gland and gills of the Yezo scallop (µg/g of protein)

Fraction	Digestive gland	Gills
Nucleus	27.8/36.8	17.1/525.6
Mitochondria	35.1/120.8	15.9/115.2
Microsomes	155.8/137.4	24.1/114.3
Cytosole	38.7/91.3	24.9/61.4

10. REPRODUCTIVE SYSTEM AND GAMETOGENESIS

The Yezo scallop is a dioecious animal. Among the males alone, we observe rare cases of functional hermaphroditism, where a few oocytes develop together with the male gametes in the genital tubules. Bisexual individuals are most common among one-year-olds, when the sex of the individual has not yet been fully established, and the indifferent gonia are capable of developing both as male and female gametes (Mori et al., 1977). The indicated authors believe that males predominate in the scallop populations at this age; some of those with unstable sexual characters begin to function as females under the influence of estrogens. At the age of about two years, the male gonads transform into ovaries, and the sex ratio balances out to approximately 1:1.

In natural populations, the Yezo scallop becomes sexually mature in its third year of life (Bazikalova, 1950; Yamamoto, 1964; Dzyuba, 1972; Kasyanov et al., 1980). During artificial cultivation, mature gametes have been found in the gonads of one-year-old males and females (Mori, Osanai, 1976). Degeneration of mature gametes have been noted by the authors in young scallops; therefore, one can assume that the scallop reaches full sexual maturity not sooner than at the age of two years.

The number of sexually mature individuals in a population can vary significantly. In the open parts of Peter the Great Gulf, its reproductive part constitutes 93-99%, while the percentage of sexually mature mollusks in the isolated bays is lower, and, according to Bregman's data (1979), varies from 59 to 88%.

The Yezo scallop is characterized by a high degree of fecundity; an average 100,000,000—170,000,000 eggs are found in the female gonad (Yamamoto,1964).

10.1. Anatomical differentiation of the gonad

The gonads of both sexes have a similar anatomical structure, and consist of a system of branching tubules that descend into a saccate arciform organ attached to the base of the foot and rounding the kidney and adductor muscle. The definitive gonads develop relatively late in the scallop. When the shell is 1.5 mm high, an intestinal loop is seen forming at the base of the foot, and a narrow layer of connective tissue enclosed by a thin wall appears around this loop; a small concentration of primary gametes is found in the apical part of this complex. A pair of strings containing the indifferent gametes descends from it parallel to the intestinal loop. Farther on, the cellular strings give rise to two central gonoducts which, branching, form a system of tubules that close in a vesicle (acinus) on the end. The formation of acini also begins in the area adjacent to the base of the foot, where the gonad is more developed than in the lower part. The paired gonoducts, connecting with the kidneys, open to the exterior (Ivanov, Strelkov, 1949).

The complex consisting of genital tubules, the intestine and connective tissue is sometimes called the visceral mass (Ivanov, Strelkov, 1949). However, as the mollusks grow, the connective tissue is retained only around the intestinal loop; in the remaining part of the complex, it is almost completely replaced by acini and efferent ducts. The complex is abundantly supplied with hemolymph as a result of its well-developed vascular system, is innervated, has an intricately structured wall, and in mature scallops begins to function in the same way as a sex organ where the genital tubules function as a parenchyma.

According to Varaksin and Deridovich (1984), an outer epithelium with an underlying basement membrane, a middle muscular—connective tissue layer and a membrane adjacent to the germinative zone can be distinguished in the gonadal membrane. Depending on the degree of maturity of the gonad, the thickness of the membrane varies from 80 to 250 μm. It is the thinnest just before spawning, and the thickest during reproductive inactivity.

The outer layer of the membrane is formed by single-layered multirow high prismatic epithelium in which at least three types of cells are differentiated, namely microvillary, ciliated and intercalary cells. A layer of multirow epithelium lies on a clearly defined 1-2 μm basement membrane. The latter consists of an amorphous substance and of the finest tightly packed fibres at the base of the epithelial cells. Their reticulum becomes looser as the membrane passes into connective tissue.

The middle muscular—connective tissue layer has a thickness of 40-200 μm. In it, we distinguish a narrow layer of connective tissue with the basic substance prevailing, a muscular layer, and a vascular layer with terminal microvessels lying adjacent to the basement membrane. Our attention is drawn to the abundance of open fissures and wide intercellular spaces in which hemolymph circulates.

The muscular layer contains myocytes, fibroblasts, and a well-developed intercellular substance with an abundance of fibrous structures. The fibroblasts and myocytes are embedded in the main substance, the fibres of which do not have the cross-striation characteristic of collagen, but form differently oriented bundles. These bundles are undulate in the gonads of spawned-out scallops, and are drawn out and straight in prespawning individuals.

The deepest layer of the inner membrane contains the terminal vascular network; in it, we encounter individual muscle cells, granulocytes containing electron-dense granules, as well as cells with a highly vacuolated cytoplasm.

The germinative zone of the gonad includes the gametes and the auxiliary cells.

The wall of the gonad in the scallop is apparently responsible for a number of its processes, i.e. the circulatory system of the wall maintains a constant medium for the developing gametes; the muscle cells, together with the connective-tissue fibres, forms a unified organ, the tone of which stimulates gametogenesis; the contractile function plays a decisive role in the spawning process. Furthermore, the alternate contractions of small groups of myocytes aid in the circulation of hemolymph in the vessels that do not have their own contractile elements. The intramural nerve apparatus of the gonad controls gametogenesis with the help of neurohormones and neurotransmitters (Motavkin, Varaksin, 1983).

10.2. Cytological differentiation of the gonad

A number of authors have studied the differentiation of the gonad in the young of the Yezo scallop (Dzyuba, 1972; Mori, Osanai, 1976; Osanai et al., 1980). It has been shown that anatomical differentiation of the gonad is slightly ahead of cytological differentiation. The criteria of cytological differentiation are definitive establishment of sex and the presence of male or female gametes in the gonad. In a one-year-old scallop, the definitive gonad is transparent, and the intestine can be seen through its wall. Histologically, the gonads are already differentiated into testes and ovaries.

10.2.1. Ovaries of sexually immature females

The oogonia and oocytes of early protoplasmic growth are found along the walls of the acini in the ovary. Both the oogonia and oocytes form local concentrations of several cells each. The oogonia consist of spherical cells 5-6 µm in diameter, containing a large bubble-like nucleus with one or two nucleoli and well-defined small lumps of chromatin. The cytoplasm of these cells is weakly basophilic and almost transparent; inclusions are not detected under a light microscope. The oogonia have a fairly high synthetic activity, and include ^{3}H-thymidine and ^{3}H-uridine thoughout all the seasons.

The oocytes of early protoplasmic growth are also spherical, with a diameter of 8-12 µm; they are not yet connected with the wall of the acinus, and are found at different distances from it. The nuclei of the cells are large (8-10 µm in diameter), and contain chromosomes in the form of distinct threads that gravitate toward the nuclear membrane and come into contact with it by their telomeres; the chromosomes are detected most commonly at the stage of leptotene and pachytene of the meiotic prophase. Cells with this type of morphology are regarded as oocytes of the 1st stage of growth.

By the second year of life, oocytes flattened out on the basement membrane of the acinus or connected with it by a short pedicle appear in the female gonads. With the formation of the pedicle, the cells extend toward the lumen of the acinus and become pear-shaped. Their maximum diameter varies from 15 to 50 µm. At this stage of growth, a nucleolus appears in the nucleus of the oocytes, the chromosomes despiralize, and the Feulgen reaction is negative. Micellar structures and granules with a high content of mucopolysaccharides, protein and RNA form in the cytoplasm. The oocytes enter the stage of vitellogenesis. As demonstrated by electron-microscopic observations, yolk formation in the oocytes of the scallop begins very early, and the yolk is at first endogenic. Microvilli form in the youngest oocytes that have entered the period of rapid growth. Pinocytotic vesicles, many of which contain an electron-dense substance, form at the base of the villi. With the growth of the cells, the length and the number of villi increase, and the number and size of the inclusions increase correspondingly. The cell enters the stage of active synthesis. When radioactive uridine is introduced into the gonad, the RNA precursor is incorporated into the nucleolus after only 30 minutes, and is detected in the karyoplasm and cytoplasm after one hour (Dzyuba, Gruzova, 1976). The oocyte begins to produce a trophic material. These cells belong to the oocytes of the 2nd stage of growth.

10.2.2. Testes of sexually immature males

Spermatogonia prevail in the gonads of sexually immature males (one-year-olds), but spermatids and spermatozoa are encountered in some cases. However, the presence of mature gametes is not necessarily an indication of sexual maturity, for the early spermatozoa undergo resorption during the period of active spermatogenesis. The spermatogonia are spherical cells measuring 7-8 μm in diameter; they contain a bubble-like nucleus with small lumps of chromatin. The nuclei activity incorporate ^{3}H-thymidine; the nucleolus abounds in RNA; the cytoplasm contains a large number of mitochondria. The Golgi apparatus is poorly developed, and consists mainly of separate smooth canals and vesicles. A large number of ribosomes are present; they often form polysomes (most commonly in the perinuclear zone). Mucopolysaccharides, glycogen and triglycerides are noted in the cytoplasm of the spermatogonia; RNA is localized predominantly in the perinuclear zone, and a low concentration of nuclear proteins is noted there. From 5 to 10% of multinucleate cells (2-5 nuclei) is encountered among the spermatogonia of the scallop during the period of their active proliferation. The multinucleate spermatogonia often contain nuclei of different size and different electron density, with a DNA concentration of 2-5 C. The multinucleate cells do not produce full-value spermatozoa; they die at different stages of development, and are therefore regarded as pathological elements.

Primary and secondary spermatocytes are another cell form in the gonads of immature males. The primary spermatocytes are slightly smaller than the spermatogonia (about 7 μm in diameter). The large globular nucleus (4-5 μm) contains compact chromatin. The single RNA-abundant nucleolus disappears at the stage of diakinesis. During the meiotic prophase at the stage of diakinesis, bivalents, which turn a bright colour with the Feulgen stain, are rod-shaped. Spermatocytes at the stage of pachyneme are the most common among the prophase cells. Autoradiographic analysis has shown that DNA synthesis is the most active in interphase spermatocytes. RNA is synthesized in the nucleus only up to the stage of pachyneme. The formation of RNA in the cytoplasm is not observed, due to which its synthetic apparatus is poorly developed. The endoplasmic reticulum consists of small and sparse smoothly-contoured vesicles and cisternae. The ribosomes do not usually form polysomes, but the intensity of the cytochemical reaction to RNA is quite high throughout the entire prophase. The Golgi apparatus consists of flat membranes and relatively large vacuoles with a transparent and dense material. Rather sudden cytochemical changes are observed in the primary spermatocytes as compared with the spermatogonia; the glycoproteins disappear completely, the lipid inclusions are preserved in trace amounts, and the concentration of the basic proteins sharply increases in the nucleus.

The secondary spermatocytes that appear as a result of the first maturation division have a short life cycle. Their nuclei measure 5-6 µm in diameter, and their cytoplasm is low in organelles and RNA. With staining by the Feulgen method, DNA is seen in the form of large granules; with the Brachet method of staining, the chromosomal threads are bluish-green. The secondary spermatocytes are characterized by a high concentration of the basic proteins. They do not incorporate the precursors of either DNA or RNA.

10.2.3. Ovaries of sexually mature females

By the end of the second—beginning of the third year of life, oocytes belonging to the 3rd stage of growth appear in the gonads of the scallop (Gruzova, Dzyuba, 1973). These are cells of a characteristic form; they are attached to the wall of the acinus by means of a more or less narrow pedicle which passes into an expanded oval part of the oocyte. Their diameter in the widest part is 50-70 µm, and the diameter of the nucleus is 25-30 µm. The heterogeneous nucleolus contains vacuoles which often fuse into one central one. This coincides with the intensification of interaction between the nucleus and the cytoplasm; the nuclear membrane becomes scalloped, and its surface becomes covered with vesicles which react strongly to RNA and proteins. Constricting, these vesicles find their way into the cytoplasm and, dispersing in it, reach the very periphery of the cell. At this stage of growth, metabolically active zones containing a multitude of mitochondria, ribosomes and highly active cytochromoxidases and succinate dehydrogenases appear in the perinuclear region of the oocyte. Due to a high concentration of RNA and protein, these areas are distinguished from the rest of the cytoplasm by a higher than usual basophilia. The ever-growing number of developing micellar structures which become concentrated around the nucleus form large strands from the apical to the basal part of the cell. As a result, the cytoplasm acquires the characteristic mosaic-fibrous structure.

Large granules of yolk are detected between the fibres. The scallop becomes sexually mature and ready for its first spawning in the third year of life. In the female gonad, the lumens of the acini are filled at this time with oocytes that have completed their growth; they lose contact with the basement membrane, reach a diameter of 80 µm, and acquire a spherical shape. In the nucleus that retains the form of a germ vesicle, spiralizing chromosomes appear at the stage of diakinesis. The nuclear membrane remains distinctly plicate; vesicles separating from it by constriction are sometimes noted. The cytoplasm of grown oocytes is filled with large yolk granules of a glycoprotein nature. The surface of the oocyte is covered with microvilli. Oocytes that have completed their growth are at the 4th stage of differentiation, and emerge from the gonad in this form during spawning. Reduction division, equation division and the formation of the pronucleus, which lead to the definitive maturation of the egg cell, take place in the environment.

10.2.4. Testes of sexually mature males

At the onset of spawning, the acini are filled with spermatozoa and spermatids. Spermatocytes are not usually present, and spermatogonia are encountered singly.

The spermatids appear as a result of the second maturation division, and are relatively long-lived elements; their size and shape depend on the degree of maturity. At the very beginning, they are spherical, with a globular nucleus (2 µm) surrounded by a narrow border of cytoplasm containing an abundance of free ribosomes. The only dictyosome with electron-dense vesicles is found near the nucleus. The mitochondria are dispersed randomly. The distal and proximal centrioles are connected to the cell membrane. In the process of spermatid differentiation, the proacrosomal vesicles of the dictyosome fuse into a single acrosomal vacuole. The latter invaginates into the anterior hemisphere of the nucleus, and turns into an elongated turbinate acrosome; the endoplasmic reticulum disappears from the cell. Chromatin condensation increases and the concentration of the basic proteins sharply increases inside the nucleus. Towards the middle of spermiogenesis, a large part of the mitochondria undergoes reduction, while the remaining five are located around the nucleus, increase in size and have well-developed crests. The distal centriole forms a flagellum. The first mature cells form in the centre of the acinus.

The spermatozoa have a small head, neck and tail. The head is formed by a nucleus with condensed chromatin containing a high concentration of the basic proteins. An acrosome is found on the anterior surface of the head. The axis begins from its posterior part; it passes through the canal, and spiralizes above the proximal centriole. The distal centriole is found at a right angle to the proximal one; it forms a flagellum with two central and nine pairs of peripheral fibrils.

According to some authors (Mori et al., 1977; Wakui, Obara, 1967), the males of the scallop attain sexual maturity sooner than the females, and can take part in spawning during the second year of life.

Both the ecology of spawning, and the dynamics of gonadal development in the scallop have been studied mainly in relation to commercial breeding of this mollusk in the waters of Japan (Yamamoto, 1950, 1951, 1952, 1955, 1964; Maru, Obara, 1973; Osanai, 1975; Maru, 1976), and later off the Soviet coast (Peter the Great Gulf, Sakhalin Is.) (Zhyubikas, 1969; Dzyuba, 1972; Kulikova, Tabunkov, 1974; Belogrudov, Maltsev, 1975; Kasyanov et al., 1980).

10. 3. Reproductive cycle

Toward the beginning of the spawning period, the gonad of the scallop is very swollen; it is pink or orange in the females, and milky white or cream-coloured in the males. The acini reach their maximum size at this time, and are separated from each other by connective-tissue septa. Most of the reproductive elements in the females consist of free oocytes that have completed their growth, and a smaller number of 3rd-stage oocytes that are connected to the basement membrane by a narrow pedicle. We occasionally encounter 2nd stage oocytes which apparently turn into egg cells only during the following reproductive cycle (Fig. 35). Mainly spermatids and spermatozoa are found in the male gonads. The asynchronous formation of ready-to-spawn gametes is responsible for intermittent spawning which lasts for approximately the same length of time in different parts of the range (1.5-2 months). Belogrudov believes that the spawning of the scallop takes place within brief periods (about 10 days) in individual areas, but lasts up to 1.5 months for the entire water area. Spawning begins earlier and ends earlier in the heated through shallow waters of bays. Spawning at a depth of over 20 m is observed from June to August. Data on the ecology of spawning in the Yezo scallop are given in table 24.

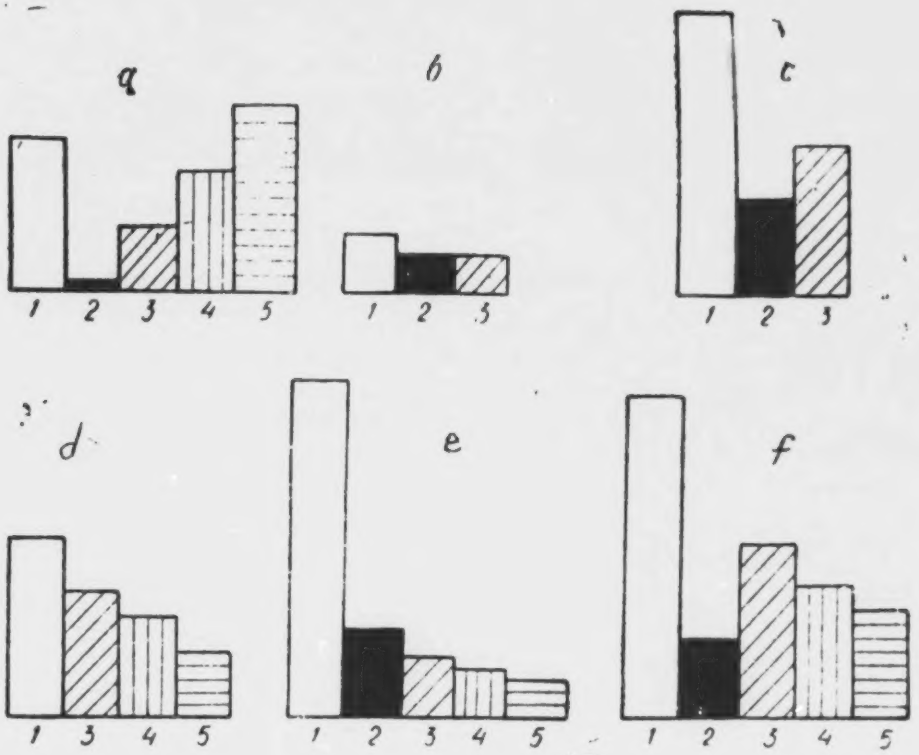


Fig. 35. Dynamics of the cellular composition of the female gonads in the Yezo scallop during different seasons. 1 - oogonium, 2 - oocyte I, 3 - oocyte II, 4 - oocyte III, 5 - oocyte IV; a - May, b - July, c - October, d - January, e - February, f - March

10.3.1. Destructive processes in the gonad

Spawning is followed by the disruption of cellular interactions, and causes profound morphofunctional rearrangements in the tissue systems of the gonad. First of all, resorption of the unspawned gametes and partial deterioration of the parenchyma take place. Necrosis of the oocytes begins with the characteristic loosening of the cytoplasm; as a result of polymerization of the lipid-protein complexes, its surface layer becomes coarsely granular and porous. The cytoplasmic membrane then undergoes lysis, and the contents of the oocyte spill into the intercellular space. With the onset of lysis or immediately following it, hydration of the nuclei begins; the nuclei swell considerably, and lose their transparency; however, spiralized chromosomes at the stage of diakinesis are easily detected in them. The resorption processes sometimes spread to all the cell elements, which results in zones of cytoplasmic material with nuclei of oocytes at different stages of degeneration. Dense nuclei of germ cells are also found in this substrate. As shown by experimental and electron-microscopic studies, the germ cells in resorption play a very important role. They distinguish the dying cells; they phagocytize and utilize the decomposition products, excreting them from the organism or breaking them down to simple chemical compounds, and secrete them into the hemolymph. As noted by Mori and coauthors (Mori et al., 1977), the degeneration of the parenchyma takes place very quickly in the scallop, and, because of the regenerative processes masking it, is not always clearly defined. Not all the acini undergo complete degeneration. For the most part, the necrotic processes involve only the unspawned gametes, while the wholeness of the membranes and the viability of the gonia and early oocytes are preserved. The histological structure of these gonads is reminiscent of the gonad of immature mollusks, but is distinguished from it by a smaller number of reproductive elements, irregularly-shaped acini and reduced connective tissue. The latter expands and thickens only around the intestinal loop, separating it from the genital tubules of the gonad. The outer wall of the gonad becomes plicate, and the empty acini make the gonad appear transparent. After spawning and the reduction of some of the parenchyma, the gonad becomes much smaller.

10.3.2. Regenerative processes in the gonad

Regenerative processes develop parallel to the necrotic changes in the gonad. They are characterized by 1) the formation of new acini, 2) the proliferation of the least differentiated gametes (gonocytes and gonia), and 3) morphogenetic processes aimed at regeneration of the stromal and feeding elements of the gonad. The gonads of mollusks belong to the slowly regenerating organs; however, the morphofunctional rearrangements brought on by spawning take place fairly quickly, and are completed in 1-2 weeks.

Table 24. Spawning of the Yezo scallop in different water areas (from: Kasyanov et al., 1980)

Spawning period, months												t °C at onset of spawning	Water area	Reference
I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII			
						—	—					-	Aniva Gulf, Sea of Okhotsk	Skalkin, 1966
					—	—	—					-	S Kurile Strait, Sea of Okhotsk	Skalkin, 1966
			—	—								9	Saroma Is., Okhotsk coast of Hokkaido	Wakui, Obara, 1967
			—	—	—	—						-	Saroma Is., Okhotsk coast of Hokkaido	Maru, Obara, 1973
			—	—	—							7 - 11	Vostok Bay (Peter the Great Gulf)	Kasyanov et al., 1976
			—	—								8 - 10	Ussuri Bay (Peter the Great Gulf)	Dzyuba, 1972
				—	—	—	—					8 - 9	Posyet Bay (Peter the Great Gulf)	Belogrudov et al., 1977
						—	—					-	Peter the Great Gulf	Bazikalova, 1950
				—	—	—	—					8 - 12	Posyet Bay (Peter the Great Gulf)	Golikov, Skarlato, 1967

Note: Unbroken line marks the periods of spawning.

The formation of acini in the post-spawning gonad takes place in the same way as during the formation of the gonad in juveniles, i.e. by the growth and branching of the genital tubules. The proliferation of gametes in them begins during spawning, and ends simultaneously with the cesssation of the destructive phenomena. Mitoses are at first detected in the newly formed acini. Cell reproduction in the rest of the parenchyma is observed in autumn (in September—October) and in February—March (with the onset of active gametogenesis). The absence in the gonads of specialized auxiliary elements that effect the development of the gametes is compensated by the corresponding function of the cells of the internal medium, specifically the germ cells. The proliferative processes in the gonad during and after the spawning period are superimposed on the suppression of neurohumoral regulation (Motavkin, Varaksin, 1979), and are presumably activated by local factors. These may be cell metabolites or substances freed as a result of their destruction.

A high reactivity of germ cells is noted during the regeneration of the gonads. It is directed at the physiological regeneration of the latter, which is triggered by the degenerative processes associated with spawning. Regeneration is based on two processes, namely the reparation of damaged structural elements and the formation of new ones. The regeneration of the gonad takes place on both the cellular and tissue levels. These processes in the reproductive cycle of the scallop reflect the special functional state of the gonads, and can be distinguished as a separate stage.

With the completion of the morphofunctional restructuring of the gonad, the mollusk passes into the state of reproductive inactivity. During this period, the gonads of the scallop are smaller, lack turgor, and are almost transparent. Oogonia and individual oocytes attached by their wide base to the wall of the gonad are found along the walls of the diminished acini. Autoradiographic analysis with ^{3}H-uridine has shown that the cells of the mollusk's gonads are characterized by a fairly high level of RNA synthesis during this period. However, the labelled precursor is incorporated only into the epithelial cells, oogonia and oocytes of the early meiotic prophase. The radioactive label is not detected in the oocytes connected to the wall. During reproductive inactivity, trophic material does not accumulate and proliferation of young gametes does not take place in the female gonad.

A small number of spermatogonia, also in the inactive state, are found in the male gonads. From the curve depicting temperature variation in Lazurnaya Bay—Ussuri Bay (Fig. 36), we see that the period of reproductive inactivity in the Yezo scallop comes in the months when the water temperature is the highest. Consequently, a high water temperature has a negative effect on the functional activity of the reproductive system in the scallop.

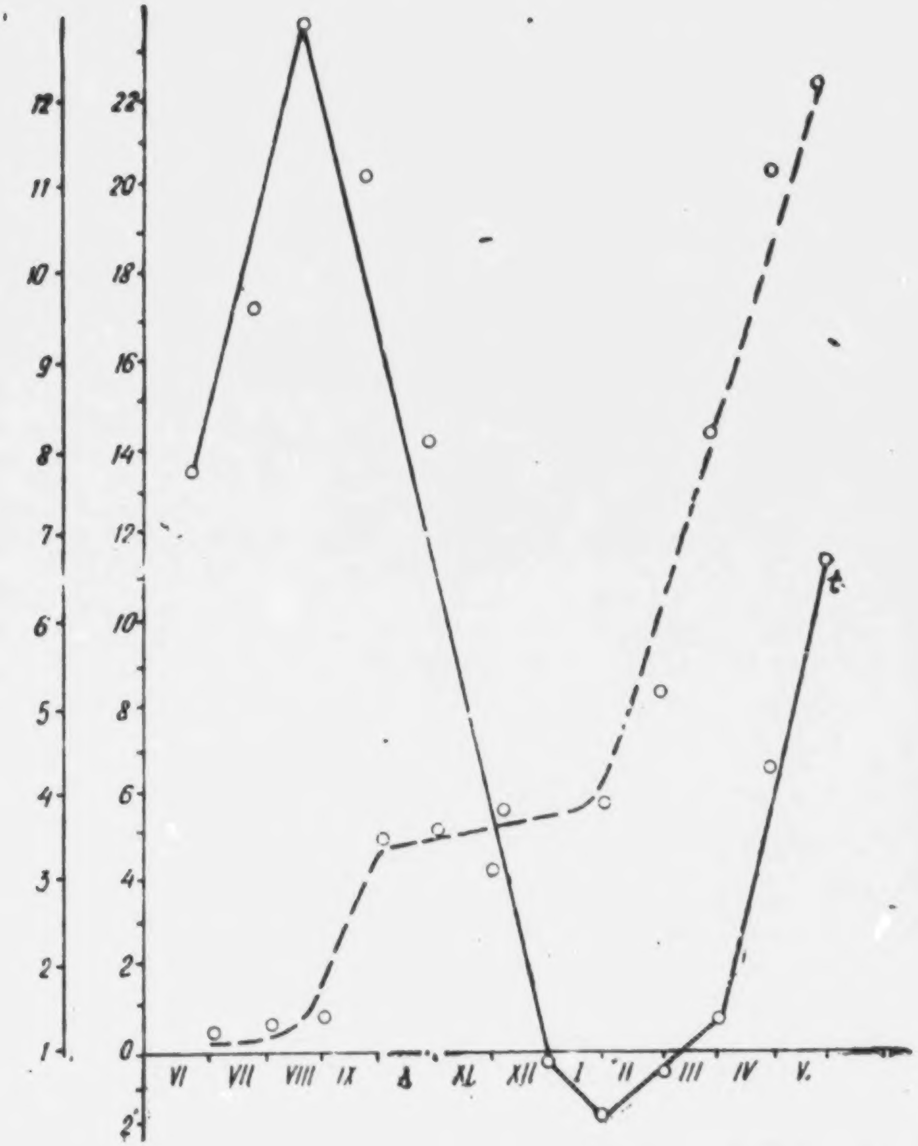


Fig. 36. Development of the gonads in the Yezo scallop. X-axis - months; Y-axis (left to right) - volume of female gametes (thou. μm^3), water temperature in Ussuri Bay (°C)

From the second half of September—beginning of October, the gonad of the scallop increases in size and becomes resilient; the acini expand and acquire a relatively regular spherical form. Proliferating oogonia appear along their walls, and the number of oocytes in the early meiotic prophase increases significantly. Differentiation of the oogonia into primary oocytes takes place in autumn; they are far more abundant in October than in other months. The oocytes of early trophoplasmic growth are inactive in summer; in autumn, they begin to incorporate the radioactive label, which appears above the nucleus after 30-minute incubation in ^{3}H-uridine. The gametes continue to develop in the ovary up to the onset of low winter temperatures (Fig. 36). During this time, some of the oocytes manage to bypass the stage of late trophoplasmic growth, and some cells reach maximum size. Synthetic processes continue in all the cells of the gonad up to the onset of winter.

The gonads of the scallop attain quite a large size by the beginning of winter. They become compact; in the female, they are bright orange, and occupy a large part of the mantle cavity. The ovaries contain a large number of oogonia, but no oocytes in the early meiotic prophase. The free-lying oocytes and a large part of the growing oocytes undergo necrobiosis. The introduction of a radioactive precursor of RNA has shown that, in winter or at any other time, the female gametes do not synthesize RNA, or else synthesis takes place very slowly in them. A decrease in DNA synthesis in the spermatogonia and the absence of mitoses among them are also noted. Definitive inhibition of spermatogenesis does not occur at this time, since premeiotic synthesis of DNA is observed in the primary spermatocytes. Differentiation of the male gametes continues because of this. Therefore, the proliferation of oogonia does not occur in the ovaries of the scallop in winter; the synthetic processes diminish, growth slows down, and some of the oocytes undergo resorption. The condition of the gonads during this period is reflected as a plateau in the graph (Fig. 36), which points to the cessation of gametogenesis.

The activation of gametogenesis in the scallop begins in February, and continues in March. During this period, the gonads increase in size and swell considerably; the number and size of the acini increase, and gametes continue to form rapidly. Oocytes in the early meiotic prophase reappear in the gonads, and yolk formation is activated in the growing cells. The average volume of the cells at this time (Fig. 36) increases significantly in comparison with the winter months, which is evidence of their high rate of growth.

Gamete resorption dies down, though destruction of some of the oocytes continues.

The size of the gonads increases in March. The acini lie close together, and the connective-tissue interlayers between them almost disappear. The formation of oogonia and the growth of oocytes intensify, and cells that have lost contact with the basement membrane appear in the lumen of the acini. At this time, the male gonads contain mostly primary spermatocytes. Spermatogonia and secondary spermatocytes are encountered singly; the synthetic processes diminish, and the gametes prepare for spermiogenesis.

In April, the gonads of the scallop occupy almost the entire mantle cavity. They are bright pink or orange in the females, and milky white in the males. The acini are highly enlarged; their walls are stretched and thinned. There are hardly any oogonia present. The number of small oocytes is insignificant. Oocytes at the final stages of rapid growth and cells that have completed their growth prevail in the ovaries. Mainly spermatids and spermatozoa are found in the testes, and cells ready for spawning are noted in them. At this time, the animals are at the prespawning stage.

10.3.3. Scale of gonadal maturity

Gonadal development in the Yezo scallop takes place in stages thoughout the year, and is seasonal. This enables us to divide the whole reproductive cycle of the mollusk into a number of stages. The condition of the gonads in some species of bivalves, including the scallop, can be determined by means of the maturity scale proposed by a number of authors (Reddiath, 1962; Takahashi, Yamamoto, 1970, etc.). At first, six stages of gonadal development were distinguished on the basis of the macroscopic and microscopic analyses of gonads from the Yezo scallop of Peter the Great Gulf (Dzyuba, 1972). It later became necessary to examine the regeneration of the gonads as a separate stage. Taking this into account, the scale of gonadal maturity for the scallop will consist of the following stages.

Stage of regeneration. The gonads are their smallest at this stage; they are translucent and limp. They contain a large number of germ cells utilizing decomposition products. New acini are forming and gonial cells are proliferating in them. Connective tissue is growing between the acini.

Stage of reproductive inactivity. The gonads do not differ in size from those of the preceding stage; they lack turgor and colour. The sex is visually indistinguishable. In histological preparations, the gonads consist of fused acini and efferent ducts embedded in well-developed connective tissue. The acini contain a certain number of oogonia, oocytes in the early meiotic prophase, and individual cells at the initial stages of rapid growth. Only spermatogonia are found in the male gonads. This stage lasts a fairly long time in the Yezo scallop from Peter the Great Gulf. It begins in the middle of June, and ends in September.

The stage of the onset of development is characterized by the mass onset of oocyte growth. The female gonads are visually pale pink; they acquire some turgor, and are about twice as large as in the first stage. The oocytes are distributed along the walls of the acini; they are fused with them by the wide base, or form a cytoplasmic pedicle. Concentrations of cells in the early meiotic prophase are often found at the base of the growing oocytes. The scallops are at this stage of gonadal maturity throughout October and November. Primary and secondary spermatocytes, and occasionally spermatogonia, are found in the male gonads.

Stage of the cessation of development. Visual observation reveals that the gonads are fairly dense, and the sex is easily determined by their colour, i.e. they are yellow or orange in the females, and cream-coloured in the males. The oocytes cease to grow. Partial necrosis of the gametes is observed. Primary and secondary spermatocytes, as well as spermatids, are found in the testes. The gonads of the scallop are at this stage of development in December and January.

Stage of active gametogenesis. The gonads become quite dense; they are yellow in the females, and milky white in the males. All the generations of gametes, from oogonia to oocytes that have completed their growth, can be encountered in the acini of the ovaries. Spermatocytes and spermatids continue to accumulate and undergo differentiation in the testes. This stage is observed in February and March.

Prespawning stage. Visual observation reveals that the gonads are swollen, and occupy a large part of the mantle cavity; they are bright orange or pink in the females, and milky white or cream-coloured in the males. The acini attain their maximum size. The ovaries contain oocytes that have completed vitellogenesis, and oocytes that have completed their growth. The testes are filled with spermatozoa and spermatids, with rare spermatogonia found only near the wall of the acinus. The prespawning stage begins in April.

Spawning stage. The scallop in Ussuri Bay spawns from the second ten-day period of May to June inclusively. At the beginning of the spawning stage, the gonad of the scallop is very dense and brightly pigmented. Highly developed acini are noted in histological sections. They are spherical, and have thinned walls. Cells that have completed their growth prevail in the ovaries, and spermatozoa prevail in the testes.

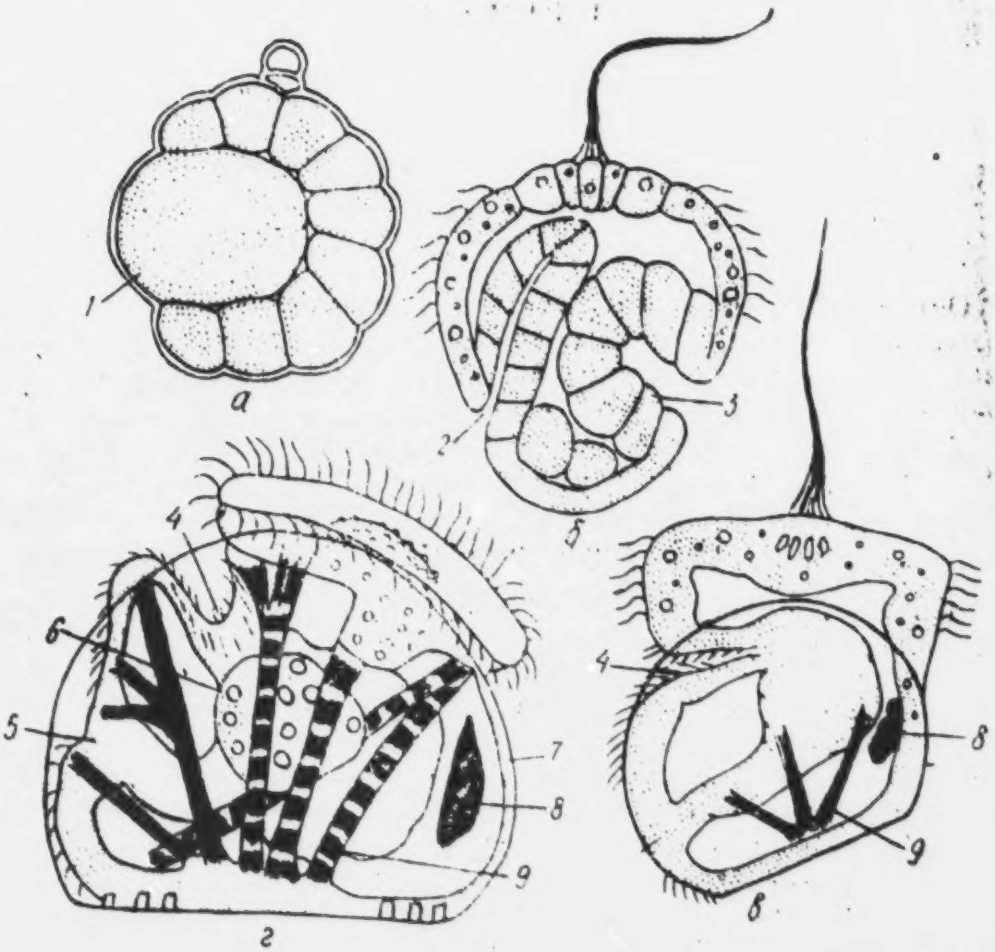


Fig. 37. Development of the Yezo scallop from the stage of sterroblastula to the stage of veliger larva (after Malakhov, Medvedeva, unpublished data): a - sterroblastula; b - gastrula, c - early veliger larva, d - later veliger larva; 1 - X blastomere, 2 - blastopore, 3 - shell gland, 4 - mouth, 5 - anus, 6 - digestive gland, 7 - shell, 8 - adductor, 9 - larval retractors

11. DEVELOPMENT

The ontogeny of the Yezo scallop has been described in a number of papers by Soviet and Japanese authors, but many of the aspects of embryonic and larval development of this species are still not clear. Therefore, the data on the development of the Yezo scallop will be augmented by the ontogenetic observations of other bivalve species, conducted by various researchers (see Kasyanov et al., 1983).

11.1. Embryonic development

The eggs of the Yezo scallop measure 60x70 µm in diameter. They contain a relatively small amount of yolk, and are surrounded by a vitelline membrane. Fertilization takes place in the water, up to the completion of the first maturation division. The first polar body is distinguished at the animal pole 5 hours after fertilization at a temperature of 9°C (Yamamoto, 1964), and three hours after fertilization at a temperature of 13°C (Pyen, Rho, 1978). The second polar body forms after that. The groove of the first cleavage division appears 7 hours later at a temperature of 13°C (Pyen, Rho, 1978), and 8 hours later at a temperature of 8°C (Yamamoto, 1964). As in other bivalves, egg cleavage in the Yezo scallop is spiral heteroquadrantal (Ivanova-Kazas, 1977). The first groove divides the egg into two blastomeres, a smaller AB and a larger CD blastomere. The second cleavage takes place 10 hours later at a temperature of 7-8°C; as a result, blastomeres A, B, C, and a larger blastomere D form. Prior to both the first and the second cleavage, a polar lobe forms temporarily at the vegetative pole; it retracts into blastomere CD after the first cleavage, and into blastomere D after the second cleavage. The material of the polar lobe, which is of great morphogenetic significance, then finds its way into the descendants of blastomere D—2d and 4d. The shell gland and the foot later form from the cells forming from blastomere 2d, and all the mesodermal derivatives form from the descendants of blastomere 4d. As a result of cleavage, a sterroblastula forms (data of V.V. Malakhov and L.A. Medvedeva) (Fig. 37, a). As in the majority of bivalves, gastrulation in the Yezo scallop takes place by invagination (Fig. 37, b).

After the formation of the mouth and the eversion of the shell gland, the gastrula becomes a trochophore. The animal hemisphere of the trochophore is fringed by the larval locomotory organ, the prototroch, which consists of a wide ring of cells with long cilia. A tuft of sensory cilia is found at the animal pole. The trochophore forms 3 days after fertilization at a temperature of 13°C (Pyen, Rho, 1978), and 4 days after fertilization at a temperature of 8-9°C (Yamamoto,1964).

11.2. Larval development

11.2.1. Veliger larva

The short-lived trochophore soon becomes the veliger larva typical of the bivalve mollusks. The animal part of the trochophore with the prototroch develops into the velum, which is fringed with cilia and serves as a swimming organ. The apical tuft of sensory cilia in the veliger larva of the Yezo scallop is reduced (Yamamoto, 1964). The body of the larva is covered with a translucent shell through which the internal organs are visible (Fig. 37, c, d).

The digestive system of bivalve larvae consists of an ectodermal fore-intestine, an entodermal mid-intestine, and an ectodermal hind-intestine. Food capture and transport to the mouth is carried out by the ciliated strings of the velum. This function of the velum is just as important as the locomotory one. Flagellate algae are the best food for the veliger larva. The mouth, located on the edge of the lower part of the velum and flanged by oral lobes in the veliger larva of the Yezo scallop (Fig. 37, d; fig. 38), leads into the oesophagus. The stomach is the next section of the digestive tract. The digestive gland constitutes two pockets of the stomach; among the other organs of the veliger larvae, it is distinguished by the large size of its cells and by its colour. Accumulations of food granules are seen in the cells of the gland. The gland of the crystalline style, which contains digestive enzymes, also opens into the stomach. The mid-intestine is located behind the stomach, and the short hind-intestine beyond that. There are no muscles in the intestinal wall, and food is apparently moved along it by the cilia.

There is no respiratory and blood circulation system in the veliger larva of the Yezo scallop. The uptake of oxygen and the elimination of carbon dioxide take place by diffusion. Substances are transported through the vast body cavity of the larva. The veliger of certain bivalves has special excretory organs, larval protonephridia (Meisenheimer, 1902; Waller, 1981). We do not know whether such organs are present in the larva of the Yezo scallop.

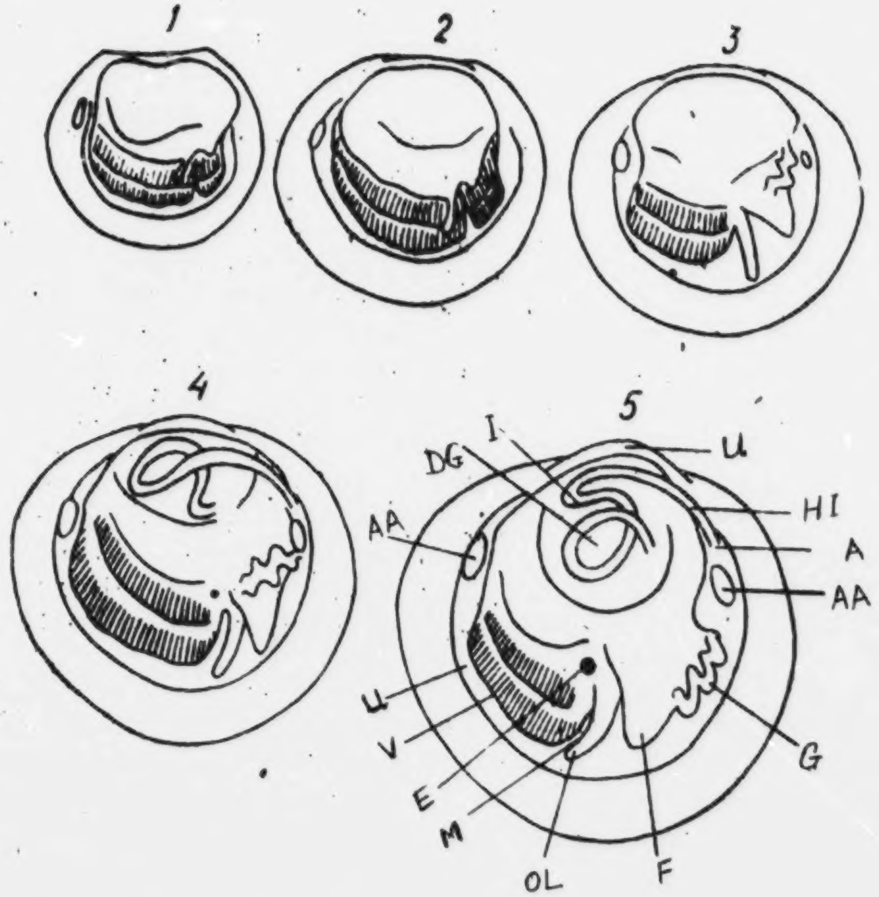


Fig. 38. Internal structure of the larva of the Yezo scallop (after Maru, 1972): 1 - straight-hinged veliger; 2, 3 - stages of umbo; 4, 5 - stages of pediveliger. A - anus, E - eye, G - gills, HI - hind intestine, U - umbo, F - foot, V - velum, AA - anterior adductor, DG - digestive gland, M - mouth, OL - oral lobe, I - intestine

The movement of a bivalve veliger larva consists of a vertical ascent followed by sinking. The veliger ascends by spreading its velum all the way and rapidly beating the cilia of the ciliated string. By decreasing the intensity of the beating, the veliger sinks. The most rapid sinking of a bivalve veliger is achieved when the velum is folded by means of the larval velar retractors and the valves of the shell are closed by the larval anterior adductor. The significant development of the nervous system consisting of the cerebral ganglion and two pedal ganglia is due to the high locomotory activity of the veliger. The apical velar plate is the main sensory organ of the early veliger.

The shell appears very early in the development of bivalve mollusks. The shell of the veliger larvae, prodissoconch I, is the product of the activity of the secretory cells of the shell gland. The valves of a fully formed prodissoconch I enclose the body of the veliger completely; they are calcified and transparent. The prodissoconch I in the veliger larva of the Yezo scallop measures 107±6.4 μm in length and 82.3±5.6 μm in height (Maru, 1972). The hinge line of the shell is straight and devoid of denticles. The valves are D-shaped. The left valve is slightly wider than the right one, but both valves are almost symmetrical in shape (Maru, 1972).

The cells of the free margin of the outer mantle fold produce a secretion which goes to form the new part of the larval shell, prodissoconch II; it is distinguished from prodissoconch I by the degree of development of the hinge, the appearance of striae on the surface (poorly discernible in pectinids), the form of the shell, and by the formation of an umbo dorsad of the hinge line in both valves of the shell. Like prodissochonch I, prodissoconch II is calcified.

The structural characteristics of the larval hinge (Fig. 39), together with the size characteristics and form of the valves, enable us to identify the species of the bivalve larvae (Rees, 1950; Chanley, Andres, 1971; Kasyanov et al., 1983). The central straight part of the larval hinge (provinculum) consists of the cardinal teeth of the hinge line of one valve and the corresponding sockets in the hinge line of the other valve. The lateral hinge system found on both sides of the provinculum is indistinct in pectinids; it consists of the thick dorsolateral margins of one valve (flanges) and the thin crests running parallel to the margins of the other valve.

There are two teeth along the margins of the provinculum of each valve in a Yezo scallop veliger with a shell length of 130-140 μm. The number of teeth increases to 3 as the length of the shell increases to 180 μm (Fig. 39).

The umbo is poorly defined in the veliger larva of the Yezo scallop (Maru, 1972).

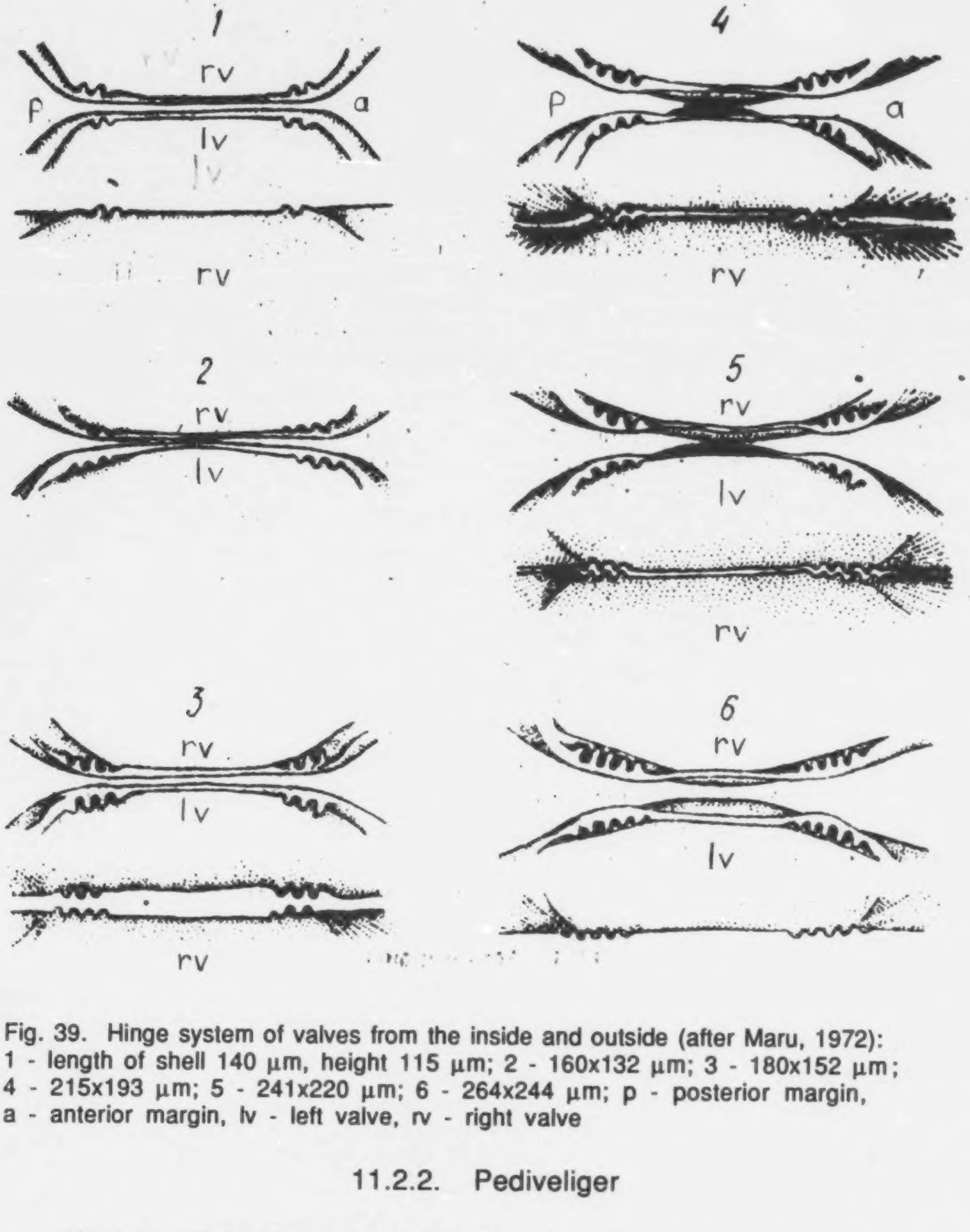


Fig. 39. Hinge system of valves from the inside and outside (after Maru, 1972): 1 - length of shell 140 μm, height 115 μm; 2 - 160x132 μm; 3 - 180x152 μm; 4 - 215x193 μm; 5 - 241x220 μm; 6 - 264x244 μm; p - posterior margin, a - anterior margin, lv - left valve, rv - right valve

11.2.2. Pediveliger

Having reached its maximum size, a larva at the stage of pediveliger has a functional foot in addition to the velum. The final goal of the pediveliger larva is to select and colonize a substrate and, having completed metamorphosis, to pass over to the definitive mode of feeding and migration.

Like most of the larval organs, the foot is a multifunctional organ. Its major functions are to search out a substrate on which the larva can settle and attach to by its byssal threads. Between the propodium and metapodium of the foot, there is a recess into which opens the duct of the byssal gland that functions temporarily in juveniles prior to the transition of an adult Yezo scallop to the free-living mode of life. As the larva swims about, the foot can be thrust out, and, on contact with a substrate, can be used to crawl along it. This may result in the attachment of the larva to the substrate, or the retraction of the foot and abandonment of the substrate in search of a more suitable one (Lane, Nott, 1975).

The sense organs of the pediveliger contribute to the search for and evaluation of a substrate. In addition to the apical plate, the pediveliger larva has statocysts and eyes. Cragg and Nott have described the ultrastructure of the statocysts in the pediveliger larva of *Pecten maximus* (Cragg, Nott, 1977). The cavities of the statocysts, which like the eyes are found at the base of the foot, first come into contact with the environment by means of openings. Then, statoliths form in the statocysts, the ducts close, and the statocysts become closed vesicles. The late larvae of pectinids, including the pediveliger of the Yezo scallop, have clearly discernible eyes in the form of dark spots that show through the shell. In the bivalve species studied in this respect, each eye is an almost spherical calyculus of pigmented epithelium filled with a gelatinous substance. The opening of the calyculus is covered with a transparent crystalline lens (Hickmans, Gruffydd, 1971).

In the pediveliger larva, prodissoconch II grows rapidly, the hinge system develops, the provinculum grows longer, and the number of teeth increases. In addition to the anterior adductor, a posterior one develops behind the visceral ganglion above the hind intestine.

The shell of the pediveliger larva is triangular-ovate. Compared with the larvae of many other bivalve species, the umbones of the Yezo scallop are small, and protrude only slightly above the hinge line. A concentric striation is clearly seen on the thin brittle shell. Five teeth are located on each side of the hinge line. Prior to the settling of the mollusks, the shell is 260-285 µm long, and the hinge line 100-110 µm long.

The formation of the byssal threads and their attachment to the substrate is the result of the functioning of the byssal glands which produce various secretions. The following types of byssal glands have been described in the pediveliger of *Pecten maximus* : 1) glands producing a very thin primary byssal thread and secondary ones; 2) glands producing mucus on the propodium and metapodium of the foot, which facilitates crawling; 3) glands producing a secretion that attaches the byssal threads to the substrate (Gruffydd et al., 1975). Neither the byssal glands, nor the behavior of the Yezo scallop during spatfall have been described in sufficient detail.

11.3. Metamorphosis

The main processes of metamorphosis are completed after the pediveliger larva finally finds a substrate and attaches to it. The larvae of marine invertebrates are selective where the substrate is concerned. The substrates on which the pediveliger of the Yezo scallop prefers to settle are listed in the next subsection. The metamorphosis of the larvae does not begin if a suitable substrate is not available. For example, the metamorphosis of *Placopecten magellanicus* can be delayed by as much as a month (Culliney, 1974). During metamorphosis, the digestive system, with the exception of the raptorial apparatus, undergoes comparatively insignificant changes (Bayne, 1971). The respiratory function passes from the nonspecialized cover tissues to the gills which at the same time function as a food capturing organ. A system of blood vessels develops after that.

The locomotory apparatus of the veliger and pediveliger, the velum, disintegrates. In the course of metamorphosis, large parts of the velum are discarded in *Placopecten magellanicus* ; only the apical part, which contributes to the formation of the upper circumoral lobe, is retained (Culliney, 1974). The larval sense organs are replaced by the definitive ones.

Changes in shell structure take place at the final stage of metamorphosis. The microstructure and mineralogy of the shell undergo change, and the layers of the new definitive shell (dissoconch) are formed (Werner, 1939). The larval hinge is also replaced by the definitive one. In pectinids, the anterior adductor of the shell is replaced by the posterior one in the course of metamorphosis.

In fast-moving mollusks, including the Yezo scallop, the attachment apparatus (foot, byssal complex) undergoes reduction at a certain time after metamorphosis.

The development of the reproductive system lags behind the development of the rest of the systems, taking place after the completion of metamorphosis. In *Mizuhopecten yessoensis* , sexual differentiation begins five months after spatfall (Osanai et al., 1980).

11.4. Distribution of the larvae and their population dynamics

11.4.1. Horizontal distribution

Currents (constant, tidal, etc.) are the decisive factor in the horizontal distribution of bivalve larvae. The more complex the overall picture of constant and temporary currents in a given water area, the more complex and unpredictable the pattern of horizontal distribution of the larvae. It is particularly complex in estuarine conditions.

Though many authors have written mainly about the passive transport of bivalve larvae, the relationship between larval distribution and the "transport systems" is quite vague, which, in Andrews' opinion, is due to the lack of hydrological research in the given areas (Andrews, 1979). Larval distribution correlates with the hydrologic characteristics of a water area to the greatest extent in the cases of entrainment water masses with low flow velocities or a high degree of stratification which limits vertical mixing (Andrews, 1979). In the Busse Lagoon, the distribution of Yezo scallop larvae is determined by the tidal and local currents; the highest density of larvae is noted during low tide in the southeastern and central parts of the lagoon where local circular entrainment currents are formed (Kulikova, Tabunkov, 1974). Larval distribution is difficult to analyze in estuaries with a high outflow of fresh water and a gradual horizontal salinity gradient.

Due to the currents, bivalve larvae circulate mainly in the water column above the parental populations and at a short distance from them, which ensures the long existence of the benthic communities (Mileikovsky, 1977). For example, in the inlets of Posyet Bay, there are more larvae of the Yezo scallop (up to 300 specimens/m^3) in the areas of scallop banks as compared with the open areas (30-60 specimens/m^3) (Belogrudov, 1981). A similar picture is observed in Mutsu Bay; the density of larvae exceeds 1000-2000 specimens/m^3 in the northeastern part of the bay where adult scallops abound (Yamamoto,1964). According to our data, the highest density of larvae (up to 230 specimens/m^3) in the Vostok Gulf of the Sea of Japan is observed in Vostok Bay which cuts deep into the land. In the neck of the gulf, there are more scallop larvae in the lower layer found in the zone of the bottom current which flows into the gulf carrying larvae from without.

11.4.2. Vertical distribution

According to Mileikovsky (1973), the larvae of benthic invertebrates that migrate vertically at a rate of 1-60 cm/min can actively occupy and retain a position in a specific water horizon in all areas except for those with a high degree of water stratification. For example, in the estuary of the James River, the larvae of benthic invertebrates are unevenly distributed vertically throughout the high-tide cycle (Wood, Hargis, 1971). According to Maru and coauthors (Maru et al., 1973), the larvae of the Yezo scallop in Lake Saroma (Hokkaido) are concentrated in the upper layers of water during high tide, and in the lower layers during low tide.

The highest abundance of Yezo scallop larvae in Posyet Bay is noted in the 4-8 m layer. The larvae are concentrated in the higher layers of water in shallower areas, and in the lower layers in deeper areas (Belogrudov, 1981). In the Vostok Gulf, there is no distinct vertical stratification of Yezo scallop larvae, or the larvae of most bivalve species, probably because of the substantial vertical water exchange. In Ionyil Bay of the Sea of Japan, the larvae of the Yezo scallop are concentrated in the bottom layers of water. In the parts of the bay with a depth of up to 24 m, 42% of the larvae are found in the bottom 4-metre layer of water, and 80% in the 8-metre layer. At a depth of 16 m, the same layers contain 50% and 90% of all the larvae respectively (Yoo, Park, 1979).

Though many believe that the density of older instars of larvae increases in the bottom layers of water (Bayne, 1976), Andrews (1979) doubts that this is a universal occurrence; he believes that the older larvae will not form concentrations at the bottom if a substrate for settling is available at other levels.

Together with the temperature and salinity gradients and the different concentration of food particles at different levels, the intensity of illumination affects the vertical distribution of the larvae. In Lake Saroma (Hokkaido), the larvae of the Yezo scallop are found mainly at a depth of 6-12 m during the daylight hours, in the 0-3 m layer before sunset, and uniformly distributed throughout the near-surface layers at night; their numbers gradually diminish in the surface layers after sunrise (Maru et al., 1973).

11.4.3. Time dynamics and density

The time dynamics and density of bivalve mollusks in the plankton depend first of all on the duration of the pelagic stage, secondly on the periods and intensity of spawning which determine the recruitment dynamics of the larval pool, and thirdly on the decrease in the concentration of larvae as a result of their entrainment from the given water area or mortality.

The periods and intensity of spawning depend on the various abiotic and biotic factors that influence gametogenesis and initiate spawning. The decisive factors are temperature and grazing conditions (Giese, Pearse, 1974). The influence of these factors is modified, and in some cases also superimposed by other factors such as salinity, lunar and other rhythms, interspecific competition, etc.

The duration of the pelagic stage depends on the temperature of the environment, the food supply of the larvae, and, towards the end of pelagic life, on the availability of a substrate for settling. If no substrate is available, the larvae delay metamorphosis and remain in the plankton (Bayne, 1976). We have no precise data on the food supply of the larvae in a natural environment (Andrews, 1979). The larval life of the Yezo scallop lasts 22-35 days at 7-13°C, 18 days at 11-13°C (Motoda, 1977; Belogrudov, 1981), and 15 days at 17-19°C (Belogrudov, 1981). The scallop requires 311-312 degree-days for the whole pelagic period from fertilization to spatfall (Gabayev, Kalashnikova, 1980). The larval development of the Yezo scallop lasts 22-30 days in Posyet Bay (Belogrudov, 1981), 20-25 days in the Busse Lagoon (Kulikova, 1979), about one month in Ionyil Bay (Yoo, Park, 1979), and approximately 40 days in Mutsu Bay (Yamamoto, 1940). According to Yamamoto, the temperature range for the development of the Yezo scallop is 6-20°C, the optimal temperature is 12°C, the salinity range is 30-40‰, and the optimal salinity is 37‰.

The larvae drop out of the plankton as a result of spatfall, entrainment out of the given area with the currents, or mortality. The causes of larval mortality are diverse. Berg (1971) lists hunger, predation, disease (primarily fungous diseases), poisoning by algal metabolites and high turbidity (small particles clog up the gills) as having a relative influence on the mortality of bivalve larvae. The specific causes of larval mortality in the plankton have not been analyzed for the Yezo scallop.

In Alekseyev Bay of Popov Is., the larvae of the Yezo scallop are found in the plankton from June to the beginning of August with a maximum density of 420 specimens/m³ (table 25); in the Minonosok inlet of Posyet Bay, they are found in the plankton for a period of two months with a maximum density of 90-190 specimens/m³ during the second—third 10-day periods of June and beginning of July (Belogrudov, 1981). In the author's opinion, the population dynamics of the larvae is determined by the spawning dynamics and the dispersion of the larvae by the currents.

In the Vostok Gulf, the larvae of the Yezo scallop are found in the plankton from the third 10-day period of June up to the beginning of August. The maximum density of larvae (60-250 specimens/m³) is observed during different periods in July, varying from year to year. In Ionyil Bay, larvae of the Yezo scallop are found in the plankton from the beginning of March up to the middle of July with the maximum noted over a two-month period from the middle of April up to the middle of June (Yoo, Park, 1979); in Mutsu Bay (N Honshu), they are found from the last ten days of March up to the last ten days of June with the maximum noted from the end of April up to the end of May at a temperature of 9-13°C. The density of the larvae varies from 2700-4600 specimens/m³ during favorable years to 170-750 specimens/m³ during unfavorable ones (Yamamoto, 1964). In the Busse Lagoon, larvae are encountered from the middle of July up to the end of August, their maximum abundance amounting to 560-1125 specimens/m³ (table 25).

11.5. Dynamics of spatfall and spat distribution

11.5.1. Choice of substrate

The pelagic life of bivalve mollusks ends in spatfall. The latter is successful only if the larva is prepared for it, i.e. all the systems required for settling should be developed and functioning. The availability of a suitable substrate is the other condition. If a substrate does not have the necessary properties, a larva prepared for settling delays doing so, and thus metamorphosis is not completed. The sensory organs developed in the late larva (pediveliger) enable it to perceive the physical, chemical and biological properties of the substrate. During spatfall, the larva perceives such physical properties of the substrate as texture, relief, colour, illumination and spatial position. However, Scheltema believes that the larva's reaction to the biological component of the substrate takes priority in the course of spatfall (Scheltema, 1974). In many cases, the substrate must be covered with a bacterial-algal film. In other cases, such a film does not affect spatfall, and even suppresses it. Scheltema believes that the species composition of the film is an important factor here. In situations where the larvae are settling on the bottom, the biological component of the selected substrate, composed of various bacteria, blue-green algae, diatoms, the early stages of brown algae and yeasts, can also play a leading part in the induction of spatfall.

The larvae of numerous bivalve mollusks settle on algae, the larvae reacting not to the algal substrate as such, but to the substances secreted by the algae into the water (Kiseleva, 1966). The larvae of the Yezo scallop prefer to settle on algae of the species *Ceramium kondoi* (Belogrudov, 1973b), *Desmarestia viridis* (Yamamoto, 1964; Kulikova, 1975), *Polysiphonia* sp., *Laminaria cichorioides* (Razin, 1934), *Heteromorpha* sp. (Bazikalova, 1950), *Sargassum pallidum, S. kjellmanium* (Golikov, Scarlata, 1970), and *Ahnfeltia tobuchiensis* (Kulikova, 1975). Seaweed *Zostera marina* (Razin, 1934), the hydroid *Obelia plana* , and polychaete cases (Yamamoto, 1964) are among the other substrates noted.

Like the larvae of other bivalves, those of the Yezo scallop are characterized by schooling; they prefer to settle on a substrate already colonized by individuals of the same species (Belogrudov, 1981).

11.5.2. Horizontal distribution of spat

The horizontal and vertical distribution of spat depends on the horizontal and vertical distribution of the late larvae, which, in turn, is largely determined, as we have already mentioned, by the hydrologic parameters of the water areas. Since bivalve larvae manifest spotty distribution as a result of a local combination of various abiotic and biotic factors, spatfall is also spotty (Andrews, 1979). The horizontal distribution of spat also depends on the distribution of the already settled individuals of the same species, the topography of the bottom, its suitability for spatfall, and, in the case of collectors, on the distribution of the latter. Andrews notes that the decisive role of hydrologic parameters in the horizontal distribution of late larvae and spat manifests itself to the greatest extent in entrainment areas. The decisive role of the hydrologic conditions upsets the relationship between the distribution of spat and the distribution of larvae; a higher rate of spatfall is noted in the areas where the density of the larvae is not maximal. The settling of the Yezo scallop in Mutsu Bay is optimal in areas with eddies, or in areas where the current velocity decreases. For example, the western shore of the gulf in the vicinity of Aomori is the most favorable for collecting spat, though the northeastern part of the gulf has the highest density of larvae (Yamamoto, 1964). The distribution of substrate (natural or artificial) perpendicular to the current is conducive to spatfall (Golikov, Scarlato, 1970). It should be said that the installation of collectors usually alters the local hydrologic conditions in a way that is conducive to spatfall (Yamamoto, 1964; Belogrudov, 1981).

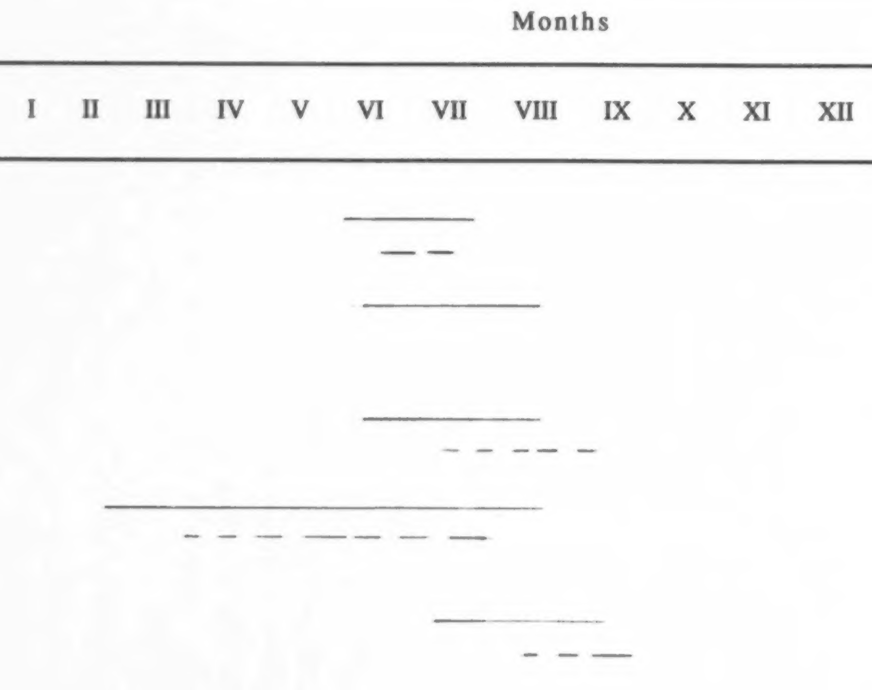
The hydrologic conditions also affect the process of spatfall itself. In Rudyakova's opinion (1981), spatfall (the author examined spatfall in *Mytilus edulis*) is basically a passive process which is similar to the sedimentation of inanimate particles from the water layer bordering on the substrate; spatfall is made easier in areas with topographic irregularities, where eddies that bring larvae to the substrate form. Emphasizing the decisive importance of hydrodynamic processes during spatfall, Rudyakova notes that the larvae, being in the boundary layer, know the distance to the substrate, since this layer contains the gradient of the horizontal component of the flow velocity; sensing this gradient, a larva can actively approach the substrate.

11.5.3. Vertical distribution of spat

The vertical distribution of bivalve spat is also affected by light, though we have not managed to establish a clear relationship between spatfall and light intensity. Andrews (1979) notes that the frequent settling on the lower surfaces of the substrate is effected not only by light, but by other factors that complicate spatfall, e.g. a layer of sludge that prevents settling on the upper surfaces. The influence of these factors may be more evident during certain years, and insignificant during others. However, despite the preference for this or that horizon or collector surface, all the suitable areas, and not only the more favorable ones, will eventually be occupied by spat if the density of larvae is high.

In Posyet Bay, the larvae of the Yezo scallop first settle in the upper horizons, but this has not been established as common for all the inlets (Maltsev, 1975). The optimal depth of spatfall in this bay is 6-16 m (Gabayev, 1981). In the Vostok Gulf, vertical settling was found to be irregular; the highest density of spat was noted at a depth of 2-10 m.

Table 25. Time spent in the plankton by Yezo scallop larvae and the periods of spatfall in different areas



Area	Reference
Posyet Bay (Peter the Great Gulf)	Belogrudov, 1981; Maltsev, 1975
Alekseyev Bay of Popov Is. (Peter the Great Gulf)	Mikulich, Biryulina, 1977
Vostok Bay (Peter the Great Gulf)	Kulikova et al., 1981; our data
Ionyil Bay (Sea of Japan coast of Korea)	Yoo, Park, 1979
Busse Lagoon (S Sakhalin, Sea of Okhotsk)	Kulikova, Tabunkov, 1974

Note: Unbroken line - time spent by the larvae in the plankton, dashed line - periods of spatfall.

11.5.4. Time dynamics of spatfall and density of spat

The time dynamics of spatfall depends on the time dynamics of the late larvae. Knowing the latter, it is easier to predict the time dynamics of spatfall if the species under study has a distinct, limited spawning period and produces a large number of larvae, and if the study area is relatively simple hydrologically. Different water areas have their own empirical formulae for determining when collectors should be set out and when the larvae of different bivalve species are expected to settle, based on the knowledge of previous spatfall patterns. There are no universal rules for predicting spatfall in any area.

Spatfall can be speeded up by increasing the temperature to a certain level and by providing a substrate for the larvae. According to Belogrudov's observations (1981), the settling of Yezo scallop larvae, which begins in the middle of June in Posyet Bay, proceeds rapidly if the sum of the May temperatures is higher than the sum of the April temperatures.

In the absence of a suitable substrate, the larvae may delay spatfall. For example, the larvae of *Placopecten magellanicus* can delay metamorphosis and spatfall for one month (Culliney, 1974). It should be said that as this delay increases, the larvae become less demanding in relation to substrate and spatfall conditions, and the range of suitable substrates and conditions broadens considerably.

The larvae of the Yezo scallop settle in the sheltered inlets of Posyet Bay from the second (sometimes third) 10-day period of June up to the first ten days of July; the length of the shell at the time of spatfall is 250-275 μm (sometimes up to 300 μm). In the open inlets of this bay, spatfall begins during the third 10-day period of June and lasts up to the first ten days of July (Maltsev, 1975). According to our data, the spatfall of the Yezo scallop in Vostok Bay lasted from July to the beginning of September; the length of the shell during spatfall was 250-300 μm. In the southern part of the Sea of Japan (Ionyil Bay), spatfall takes place from the beginning of April up to the end of June, peaking in mid May—beginning of June (Yoo, Park, 1979). In Mutsu Bay, the larvae of the Yezo scallop settle from the first ten days of June up to the third 10-day period of July with a shell length of about 300 μm (Yamamoto, 1964). In the Busse Lagoon, the larvae settle in the first half of August with a shell length of 250-270 μm (Kulikova, Tabunkov, 1974; table 26).

The density of spatfall depends on larval recruitment on the one hand, and on spat losses resulting from detachment or mortality on the other. The larvae of some mollusks, e.g. various species of oysters, attach to the substrate once and for all; the juveniles of the Yezo scallop stay attached to the substrate for 1.5-4 months, and then pass on to a free mode of life. In Mutsu Bay, the scallops attach to the substrate for 40-60 days, from the first ten days of June to the third ten-day period of July. While attached, the juveniles grow rapidly, their shell reaching a length of 10 mm. In Posyet Bay, the length of the shell increases to 15-25 mm in 60-90 days (Belogrudov,1981). According to Yamamoto, the life of the Yezo scallop during this period consists of continuous detachment from the substrate and the search for a new one (Yamamoto, 1964).

Spat losses are caused by various factors. Belogrudov (1981) writes that juvenile *Asterias amurensis* settling on collectors can destroy up to 90% of the Yezo scallop spat in Posyet Bay. One juvenile *Asterias amurensis* consumes an average 18 settled scallops (Gabayev, 1981). Abrupt temperature changes, storms (Kohara, Maru, 1970), excessively high temperatures (over 20°C) and high turbidity (Yamamoto, 1964) are detrimental to spat. The highest mortality of spat, in some cases up to 80-100%, is noted during the period of detachment.

12. GROWTH

12.1. Methods of studying linear growth

Various methods are used to determine the age and the rate of linear growth in the Yezo scallop from natural habitats; these methods have certain limitations, and sometimes produce inconsistent results. Initially, the age of the scallop was determined by the number of rings on the lower valve, or the number of dark bands on the ligament; these were regarded as annual structures (Bazikalova, 1934). One should take into account that not one, but several rings may form on the shell or ligament in a year as a result of a growth disturbance. Therefore, age determination by these methods may produce a higher than actual age and a lower than actual rate of growth.

The age and growth of the scallop are also determined in other ways, e.g. by the size structure of the population using Petersen's method, and by a modified version of this method (Tibilova, Bregman, 1975). These methods are time-consuming, and do not always produce unambiguous results. Biogeochemical methods also enable us to study the individual dynamics of linear growth in the scallop. They are based on the linear dependence of the shell's content of indicator elements on the temperature of the environment. In samples of shell calcite taken from the growth rings from the umbo to the lower margin, we consistently observe cyclic fluctuations in magnesia, the calcium/magnesium ratio (Ca/Mg) (Krasnov, Pozdnyakova, 1982; Silina, Pozdnyakova, 1982) and the ratio of oxygen isotopes ($^{18}O/^{16}O$) (Ignatyev et al., 1976). These indices reflect the seasonal changes in environmental conditions, primarily water temperature. Having counted the number of complete magnesia cycles, or the number of minimal Ca/Mg values and/or $^{18}O/^{16}O$ values, and having measured the distance from one peak of magnesium content to another, one can determine the age of the mollusk and the annual increments of its shell. From the age of 6-7 years, the annual increments of the valves are insignificant; therefore, it is difficult to get several samples from each annual layer, which complicates age determination (Silina, Pozdnyakova, 1982).

One of the most reliable methods of age and growth rate determination in mollusks is based on the periodicity of alternation of the shell's calcite and aragonite layers of different thickness.

However, the shell in pectinids is lamellar, entirely calcitic, and the growth layers are not visible in cross-sections (Zolotarev, 1976; see also section 3). Meanwhile, a regular alternation of areas with wide and narrow elementary growth layers is noted on the surface of the upper valve in the Yezo scallop (Fig. 40). It has been established that the wide layers (20 on the average) form from the middle of November to April, while the narrower ones (160-200) form during the rest of the year, the narrowest forming in July—September when the water temperature is at its highest (Silina, 1978). These data were derived by comparing the linear increments at the margins of the shell in mollusks fixed at a different time of the year, and were confirmed by determining the oxygen isotope and Ca/Mg ratios (Fig. 41). The layers formed during the cold part of the year take the form of bands with even margins; their surface is often tubercular (especially in the young of the year); the tubercles are staggered from one layer to the next; the winter segment of the valve is sometimes smooth, without distinct layers. The summer layers have a squamate structure, and draw closer together during the hottest period. With the onset of sexual maturity, the growth rate decreases, and because of this, the part of the shell with concentrations of layers begins to constitute more of the annual increment. After three years, the number of layers in the scallop is much smaller than 200. This is due to the fact that the edges of the shell often break off during spawning, and during its regeneration, the layers come close together and become indistinguishable.

During a comparison of the monthly winter increments of underyearling scallops cultivated in cages, we found that 4-6 wide elementary layers appear in one month during the cold period of the year (one layer in 5-7 days). Depending on the temperature conditions, 10-20 layers narrower than the winter ones form in May in the scallops off the coast of Primorye. May is probably the time of transition from the rhythm of layer accretion lasting many days to a diurnal rhythm of layer accretion. For example, up to 20 layers form in a young scallop of Posyet Bay in 180-200 days, from the first half of May up to the middle of November (Silina, 1978). The correlation between the time it takes a layer to form and the temperature of the water was established by the method of oxygen isotope thermometry. The transition from a diurnal rhythm of layer accretion to one lasting many days occurs in November at a temperature of 4-6°C (up to 20 layers appear during this month, and only 4-11 layers the following month).

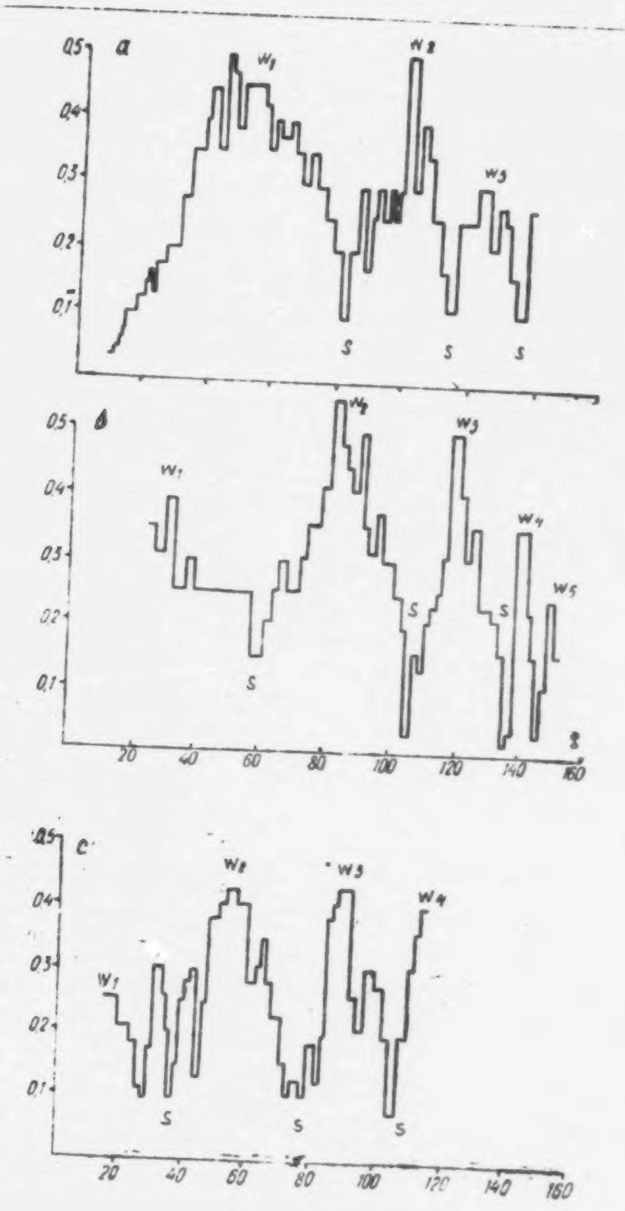


Fig. 40. Seasonal changes in the width of the elementary growth layers of the upper valve of the shell in the Yezo scallop: a - from Mutsu Bay, Honshu (southern part of the range), b - from Posyet Bay near Furuhelm Is., c - from Vladimir Gulf (northern part of Primorye. X-axis - distance from apex of shell, mm; Y-axis - width of elementary growth layer, mm; w - winter, s - summer

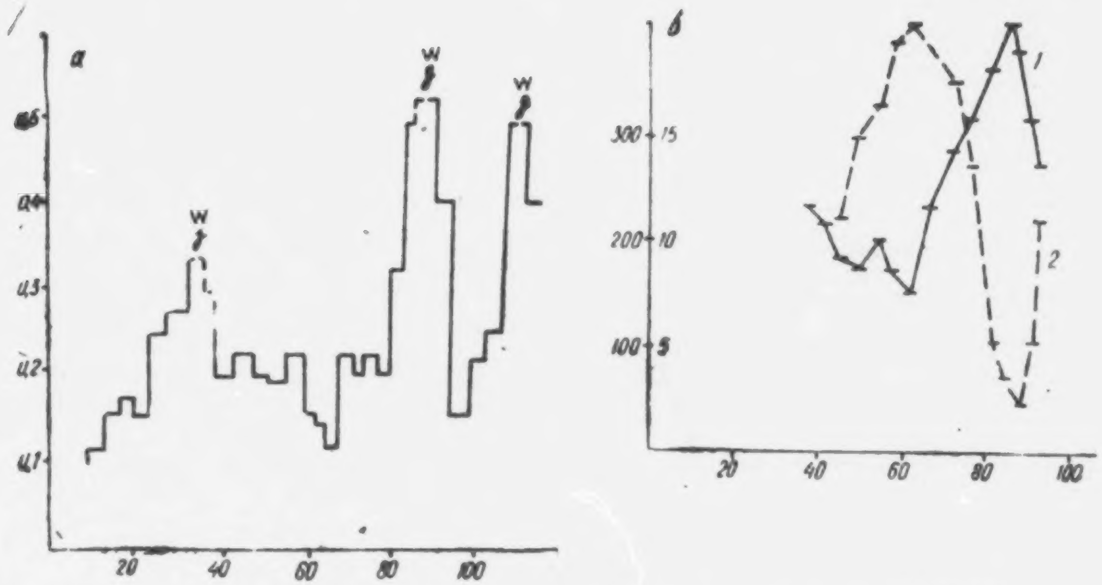


Fig. 41. Seasonal changes in the width of the elementary growth layers (a), Ca/Mg (b,1) and growth temperature (b,2) of the Yezo scallop from the Novgorodskaya inlet (Posyet Bay, Sea of Japan). Growth temperature determined by the method of oxygen isotope thermometry. X-axis - distance from the apex of the shell, mm; Y-axis: a - width of elementary growth layer (mm), b - Ca/Mg values on the left, temperature (°C) on the right. Dashed line marks winter growth layers of many days (w)

A slowing of the growth rate occurs most commonly in 3-year-old individuals spawning for the first time; it is marked by a small concentration of layers (approximately 10 increments) on the valve. In older mollusks, spawning is usually accompanied by breakage of the shell margin. After four years, the shell will bear an alternation of wide layers that had formed over a period of many days, traces of spawning breakage, and concentrations of daily increments.

Knowing the characteristics of the seasonal alternation of wide and narrow growth layers on the upper valve of the scallop, one can determine the time of their formation. At the end of July—beginning of August, a dark band appears on the ligament and on the lower valve of the shell, and a concentration of growth layers appears on the upper valve. It is at this time that the young of the year begin to settle on the bottom off the coast of Primorye. By measuring the distance from the apex of the valve to the required concentration of growth layers, we can determine the height of the shell at the corresponding age.

By studying the growth process using the method based on the characteristics of layer growth, we can derive not only a more accurate age and annual growth rate for different populations, but also the year-round characteristics of shell formation determined by environmental and internal conditions. The results presented below were derived by studying the surface sculpture of the upper valves. The ligament method of age determination was used only in the case where the upper valve was damaged or the growth layers were obliterated. The size of each shell was established for the preceding years as well. These data were used to determine the group linear growth of the population in order to calculate the mean values of shell height for specific ages of the scallop.

12.2. Linear growth

12.2.1. Ontogenetic changes in the growth rate

The highest absolute diurnal increments of the shell in the Yezo scallop were noted during its second spring—autumn period (Fig. 40). The increments that occurred over a period of many days were maximal during the second winter. During the first three years, the shell of the scallop increased in height by 12-28% of the total annual increment from November to April.

The height of the shell increases the most (to 90-100 mm) at the juvenile stage, especially during the first two years of life. The increments of the first and second years are usually almost equal, amounting to 38-48 mm each year. The populations inhabiting the marginal zones of the range are an exception. With the onset of sexual maturity (in the third year), the growth rate of the scallop decreases, but is still substantial, e.g. 22-27 mm a year off the coast of Primorye. The shell increment in the fourth year decreases 1.5—2-fold in comparison with the third year. This occurs as a result of a decrease in the absolute diurnal increments and the increments of many days, the delays of the linear growth rate, or the shell breakage during spawning. With further growth, the growth rate decreases asymptotically (table 26), and after 6 years does not usually exceed 5 mm per year.

The decrease in the growth rate of a sexually mature scallop makes it very difficult to determine its age. It is usually impossible to group the scallops into age classes without further examining the individuals with a shell height of more than 100 mm. For example, a scallop measuring 120 mm in height from Lake Vtoroye of Nakhodka Bay may be 3, 4, 5, or even 6 years old. It is especially difficult to establish age classes for populations from waters that warm up (Fig. 42).

Table 26. Annual linear increments (mm) in the shell height of the Yezo scallop with age

	Average annual shell increment at age (years)							
Area	0 - 1	1 - 2	2 - 3	3 - 4	4 - 5	5 - 6	6 - 7	7 - 8
Mutsu Bay								
Honshu Is.	84.3±2.4	33.2±2.0	10.7±1.0	5.1±0.5	-	-	-	-
Peter the Great Gulf								
Furuhelm Is.	50.2±1.2	51.2±0.9	24.5±1.0	15.5±1.0	10.4±0.8	4.6±0.8	-	-
Posyet Bay								
Pemzovaya Bay	45.1±1.0	41.6±1.0	22.3±1.0	12.9±0.8	-	-	-	-
Ekspeditsiya Bay	47.4±1.5	45.3±1.0	23.5±0.8	12.2±0.5	-	-	-	-
Novgorodskaya Bay	56.6±2.4	40.4±2.0	23.0±1.8	14.1±1.4	4.9±1.0	-	-	-
Vityaz Bay	47.1±1.3	42.1±1.1	27.0±1.0	14.4±0.8	9.7±0.6	5.5±0.4	-	-
Stenin Is.	44.6±1.2	45.3±1.2	30.3±1.0	18.1±1.0	11.9±0.9	8.5±0.8	-	-
Bolshoi Pelis Is.	-	-	30.5±1.0	18.7±2.0	8.7±1.8	-	-	-
Ussuri Bay								
Priboynaya Bay of Popov Is.	51.2±1.0	47.4±1.0	25.9±0.8	12.9±0.7	8.4±0.6	-	-	-
Shkot Is.	42.8±2.1	44.3±1.3	26.8±1.0	14.4±0.9	10.2±0.7	-	-	-
Lazurnaya Bay	43.4±1.9	37.4±1.9	23.8±2.2	16.5±2.0	6.9±1.6	-	-	-
Andreyev Bay	46.9±0.8	38.9±1.0	21.2±1.0	11.8±1.0	5.6±0.9	3.6±0.8	2.4±0.6	3.0±0.8
Putyatin Is.	50.7±1.6	40.2±1.4	24.5±1.2	13.2±1.1	7.3±1.2	-	-	-
Nakhodka Bay								
Lake Vtoroye	42.2±0.6	38.6±0.7	24.2±0.7	15.4±0.7	10.4±0.6	7.4±0.5	0.8±0.1	3.0±0.4
Melkovodnaya Bay	44.2±1.8	39.2±1.5	26.4±1.3	19.8±1.1	10.5±1.0	9.3±0.9	-	-
Olga Gulf	36.6±2.0	43.8±2.2	30.4±2.0	14.0±1.6	11.0±1.3	-	-	-
Vladimir Gulf, Sakhalin Is.	33.6±2.0	43.8±2.2	30.4±2.0	14.0±1.6	11.0±1.3	-	-	-
Aniva Gulf (near Kirillovo settlement)	26.1±2.0	30.1±2.0	30.7±1.8	24.0±1.6	14.6±1.4	8.7±1.0	9.4±0.8	4.8±0.6

Note: Determinations based on the surface sculpture of the upper valve of the scallop (our own data for 1976-1982), annual increments from August of one year to August of the following year.

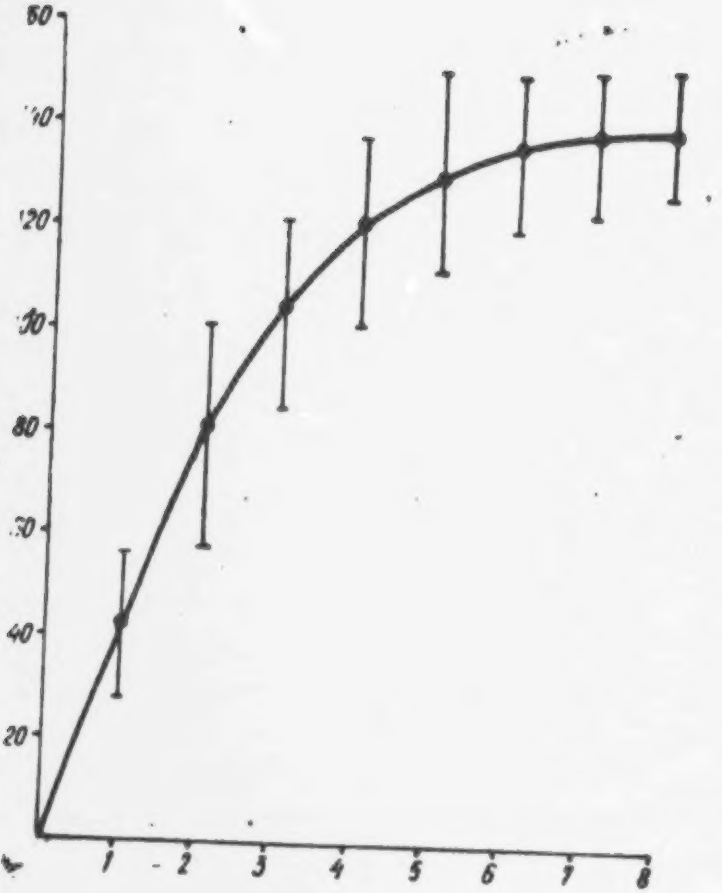


Fig. 42. Linear growth of the Yezo scallop in Lake Vtoroye of Nakhodka Bay in the Sea of Japan. X-axis - age, yr; Y-axis - height of shell, mm

12.2.2. Growth in different populations

The general growth rate tendencies of the scallop in the course of its development may change significantly with the environmental conditions, which leads to noticeable interpopulational differences in the annual increments (tables 26, 27; Fig. 40).

Table 27. Linear growth (mm) of the Yezo scallop

			Height of shell		
Area	Depth, m	Substrate	1	2	3
Honshu Is.					
Mutsu Bay	35	-	84.3±2.6	117.5±2.4	128.2±2.0
Peter the Great Gulf					
Furuhelm Is.	10-12	Sand	50.2±1.2	101.4±1.2	125.9±1.3
	-	-	-	-	118
	-	-	-	-	-
Posyet Bay					
Pemzovaya Bay	-	-	45.1±1.0	86.7±1.1	109.0±1.3
Ekspeditsiya Bay	6-8	Silt	47.4±1.5	92.7±1.8	116.2±1.4
	2-4	Boulders, sand	49.3±2.5	86.4±2.0	105.4±2.1
Novgorodskaya Bay	3	Silt	56.6±2.4	97.0±2.5	120.0±2.4
Haloway Bay	7	Silt	46.0±2.3	90.0±2.5	116.6±2.2
	-	-	-	98	115
	-	-	-	-	-
Vityaz Bay	8	Silted sand	47.1±1.3	89.2±1.1	116.2±0.9
Troitsy Bay	-	-	50	87	102
Stenin Is.	14	Sand	44.6±1.2	89.9±1.5	120.2±1.4
Bolshoi Pelis Is.	5-6	Pebbles	-	89.9±4.2	120.4±3.2
Amur Gulf					
Severnay Bay of Slavyansky Bay	-	-	53	81	105
Narva Bay	-	-	42	83	106
Entrance to Starka Str.	18	Silted sand	48.3±2.6	95.5±2.0	122.1±1.6
Reineke Is.	-	-	48	83	110
Ussuri Bay					
Priboynaya Bay of Popov Is.	12	Coarse-grained sand	51.2±1.0	98.6±0.8	124.5±0.6
Shkot Is.	8-9	Coarse sand	42.8±2.1	87.1±1.7	113.9±1.3
	7-8	Silted sand	50.9±1.4	94.0±1.3	116.4±1.4
Lazurnaya Bay	6	Rocks, sand	43.4±1.9	80.8±2.3	104.7±2.2
Andreyev Bay	7	Silt	46.9±0.8	85.8±1.0	107.0±1.0
	-	-	45	78	103
Cape Zeleniy	-	-	53	82	104
Rifovaya Bay	-	-	49	78	102
Putyatin Is.	8	Silt	50.7±1.6	90.8±1.2	115.3±1.0
Strelok Strait	-	-	50	88	113
Vostok Bay	-	-	47	83	102
Nakhodka Bay	-	-	38	68	90
Lake Vtoroye	3-5	Silt	42.2±0.6	80.7±0.7	104.8±0.6
Melkovodnaya Bay	6	Silted sand	44.2±1.8	83.2±1.3	109.6±1.4
Sokolovskaya Bay	-	-	-	-	117
Olga Gulf	10-12	Silted sand	36.6±1.1	83.2±1.4	114.6±1.4
	-	-	-	76	-
Vladimir Gulf	15-20	-	33.6±2.6	77.4±2.8	107.8±2.4
Sakhalin Is.					
Aniva Gulf (near Kirillovo settlement)		-	26.1±2.4	56.2±2.1	86.9±2.0

at the age of (yr):							
4	5	6	7	8	9	10	Method
133.3±1.8	-	-	-	-	-	-	S
141.4±1.9	151.8±1.8	156.4±2.5	-	-	-	-	S
146	165	176.5	183	-	-	-	SS
-	130	142	152	160	166	-	SS*
121.9±1.2	-	-	-	-	-	-	S
128.4±1.5	-	-	-	-	-	-	S
115.8±2.0	-	-	-	-	-	-	S
134.1±2.5	139.0±2.6	-	-	-	-	-	S
131.0±2.2	138.3±2.6	-	-	-	-	-	S
132	145	153	-	-	-	-	SS
-	130	140	148	154	-	-	SS*
130.6±1.1	140.3±1.5	145.8±2.7	-	-	-	-	S
118	130	-	-	-	-	-	SS**
138.3±1.6	150.2±2.3	158.7±2.4	-	-	-	-	SS
139.1±2.1	147.8±2.4	151.5±2.6	151.8±2.8	-	-	-	S
123	130	-	-	-	-	-	LV
123	133	149	149	152	155	-	LV
141.5±1.8	152.0±2.9	-	-	-	-	-	S
125	134	140	145	149	156	-	LV
137.4±1.0	145.8±1.9	-	-	-	-	-	S
128.3±1.4	138.5±1.9	-	-	-	-	-	S
128.5±1.5	-	-	-	-	-	-	S
121.0±2.3	127.9±1.7	-	-	-	-	-	S
118.8±1.1	124.7±1.3	128.3±1.1	130.4±1.5	133.5±1.7	-	-	S
116	123	133	137	138	147	151	LV
117	127	134	139	-	-	-	LV
120	134	142	150	161	168	174	LV
128.5±1.1	135.7±1.8	141.1±1.0	-	-	-	-	S
130	134	-	-	-	-	-	L
115	123	131	138	141	151	-	LV
104	115	129	139	143	145	-	LV
120.2±0.7	130.6±1.1	137.7±1.0	137.9±1.6	141.5±1.6	-	-	S
131	143	152	-	-	-	-	SS
129.5±1.3	140.0±1.5	149.2±2.7	-	-	-	-	S
138	149	158	-	-	-	-	SS
133.8±1.0	145.4±0.9	152.0±1.1	154.5±1.1	155.4±1.5	158.8±1.7	-	S
120	137	154	168	-	-	-	SS
121.8±2.8	132.8±2.8	-	-	-	-	-	S
110.9±1.4	125.5±1.6	134.2±2.1	143.6±2.2	148.4±2.3	156.2±2.3	160.8±2.5	S

The differences in growth rate in the coarse of biological development are particularly evident in the scallop from areas with different temperatures. The highest increments are observed within the first 1-1.5 years in mollusks from waters that warm up (table 26 - Mutsu Bay, the Novgorodskaya inlet of Posyet Bay). The increment is particularly significant during the first summer—autumn of the scallop. The opposite is observed in cold-water areas (table 26). With a relatively small rate of growth within the first two years, the increment here in the third year either does not diminish, or does so insignificantly, and then slowly decreases in the years that follow. According to Razin's data (1934), sexually immature scallops at a depth of 6-18 m in Peter the Great Gulf grow somewhat more rapidly than at greater depths (18-30 m) in the more northerly areas. For example, the mollusks of older generations grow better from Cape Povorotny to the Olga Gulf.

The linear growth of the Yezo scallop in different populations of Peter the Great Gulf (table 27) depends not only on temperature, but on other environmental factors as well. Significantly better growth, especially from the third year, is observed in the scallops around the Furuhelm, Stenin, Bolshoi Pelis, Popov and Russkiy islands, i.e. areas with a predominantly sandy or pebbly bottom, sometimes with a small admixture of silt and coquina. These 10—14-metre areas are connected with the open sea, which ensures good aeration of the water and optimal oxygen content; the salinity in summer is relatively constant and high, and the water warms up uniformly in July—August. Linear growth is slower in the populations inhabiting silty areas (Andreyev Bay, Lake Vtoroye, etc.), as well as small sandy islets amidst boulders and rocks (Lazurnaya Bay, Ekspeditsiya Bay), mostly at a depth of 5-8 m (table 27). The areas with a silty bottom are usually located in sheltered and semi-sheltered bays, and in the innermost parts of gulfs. Here we observe more drastic and frequent changes in water temperature and salinity even within a day; the water has a lower oxygen content, and the suspended particles of silt make it difficult for the mollusk to breathe. The valves of a scallop from a sandy area with rocks and boulders bear a multitude of marks of shell damage and breakage due to collision with the rocks.

Note to table 27: Values of shell height for each age determined at the beginning of August on the basis of the sculpture of the upper valve (S) (our own data for 1976-1982), the size structure (SS) of populations with the help of probability paper (Mandryka, 1979), Bregman's modification of the latter (SS*) (1979), Tibilova and Bregman's modification (SS*) (1975), the number of dark bands on the lower valve (LV) (Biryulina, Rodionov, 1972), and by the number of bands on the ligament (L) (Bazikalova, 1934).

12.2.3. Maximum dimensions and age

In populations living off the coast of Primorye on sandy substrates in relatively unsheltered areas, the scallop can grow to a height of 190-192 mm. A scallop from silted sand or pebbles usually has a shell height of up to 171-178 mm. The height of the shell in mollusks from a silty or rocky-sandy substrate does not exceed 147-156 mm. The oldest individuals reach an age of 16 years on sandy and pebbly substrates, and not more than 10-12 years on a silty substrate (table 28).

Two of the oldest scallops, 20-22 and 18 years old, were found in the Olga Gulf. Fifteen- and sixteen-year-old scallops were encountered near the Furuhelm and Stenin islands. Fourteen- and fifteen-year-olds are also quite common. The oldest scallops are usually not the largest (table 29). This difference is particularly significant in the populations found on a silty substrate.

The largest scallops (with a shell height of 192 mm) examined by us were found off Furuhelm Is. and in the Aniva Gulf (near the Kirillovo settlement). However, this is not the largest size for the Yezo scallop. Mollusks with a shell height of about 21 cm have been caught in the same Aniva Gulf (Skalkin, 1966). The largest scallops (shell height 22 cm) were caught by Skalkin (1966) in the S Kurile shallows.

12.2.4. Effect of temperature

It has been established by different methods that the linear growth of the scallop takes place at a water temperature of -2 to 26°C. At the same time, the growth range in different parts of the range correspond to the variation range of water temperature in these areas. The shells grow throughout the year. It was once believed that the scallop ceased to grow in winter (Bazikalova, 1934; Tibilova, Bregman, 1975). It was recently established that the linear growth of the mollusk did not cease at a temperature of 4-6 to -2°C, but only slowed down and became more uniform (Silina, 1978) (Fig. 43). During the other seasons, its growth now accelerates, now slows down as the temperature changes.

At a temperature below 4°C in November—April, the young of the year in the cages in Posyet Bay grow by an average 0.04-0.08 mm daily (Fig. 44), forming one wide growth layer in 5-7 days. At 4-6°C in the first half of May, the diurnal growth layers of the shell begin to form. The underyearlings grow by an average 0.1-0.2 mm daily (Fig. 44, b). Maximal growth takes place from the end of May to the middle of July at a temperature of 8-16°C; the underyearlings grow by 0.2-0.4 mm daily (Fig. 44, c). At a water temperature higher than 16°C, the growth rate slows down, amounting to 0.02-0.05 mm daily in one-year-old scallops (Fig. 44, d). At a temperature of 8-16°C, the one-year-olds grow in height by 0.2-0.4 mm from the second half of September up to the end of October (Fig. 44, e); at 8°C and lower (at the end of October), the rate of growth decreases. At this point in time, we observe a rapid transition from the diurnal rhythm of accretion of layers (which form under conditions conducive to linear growth) to a rhythm of several days.

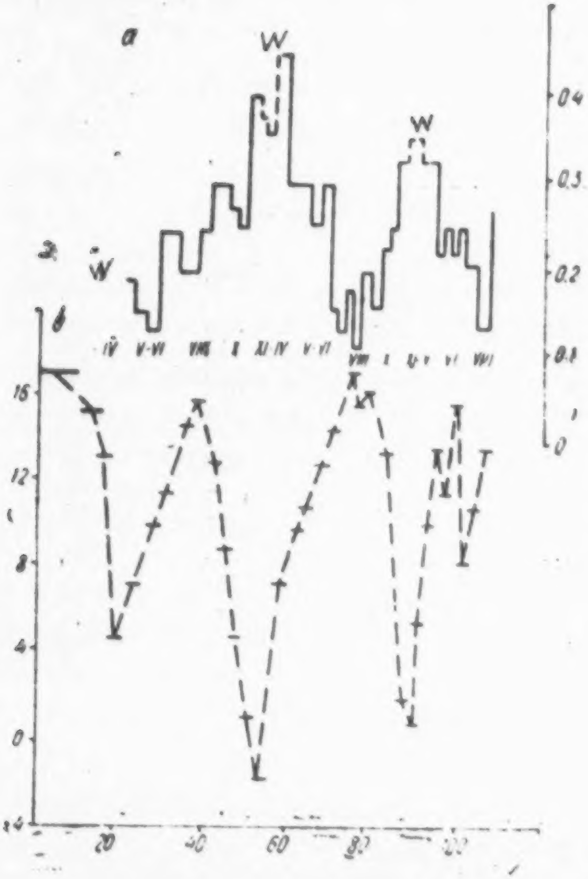


Fig. 43. Seasonal changes in the width of the elementary growth layers (a) and growth temperature (b) of the Yezo scallop from the Vladimir Gulf of the Sea of Japan from a depth of 2-3 m, established by the method of calcium-magnesium thermometry. X-axis - distance from the apex of the shell, mm; Y-axis: a - width of elementary growth layer (mm), b - temperature (°C). Roman numerals denote the months in which the corresponding part of the shell was formed (determined by the elementary growth layer). Dashed line in (a) marks winter growth layers of many years (w)

Table 28. Parameters of individual Yezo scallops with the highest shell or highest age in the population

Habitat	Height, mm	Total mass, g	Mass of shell, g	Mass of soft tissues, g	Age yr
Peter the Great Gulf					
Posyet Bay					
Furuhelm Is.	192	856	450	260	14
	176	-	367	-	16
Ekspeditsiya Bay	147	426	187	129	8
	140	465	215	123	11
Vityaz Bay	172	622	338	309	8
	163	680	359	254	13
Stenin Is.	190	863	407	282	13
	175	720	348	256	16
Bolshoi Pelis Is.	177	-	355	-	12
	164	-	307	-	15
Ussuri Bay					
Shkot Is.	169	683	371	203	13
	163	582	309	157	14
Lazurnaya Bay	150	608	319	158	14
	133	480	219	125	14
Andreyev Bay	147	378	162	116	8
	135	401	182	105	12
Putyatin Is.	156	497	225	167	8
	143	482	245	132	11
	133	439	190	112	12
Nakhodka Bay					
Lake Vtoroye	156	474	234	143	7
	150	641	303	213	10
Melkovodnaya Bay	171	787	432	304	14
	170	572	338	168	8
Olga Gulf	178	648	349	193	11
	157	643	360	159	20-22
	169	785	402	212	18
	148	520	-	168	15-17
Sakhalin Is.					
Aniva Gulf (near Kirillovo settlement)	192	-	-	-	13
	173	-	-	-	14-15
Aniva Gulf*	210	-	-	-	-
Terpeniye Gulf*	190-200	-	-	-	-
Aleksandrovsk Bay*	190-200	-	-	-	-
S Kurile shallows*	220	Greater 958	Greater 473	Greater 90	-

Note: Table contains our own data for 1974-1981, as well as Skalkin's data marked by asterisk (1966).

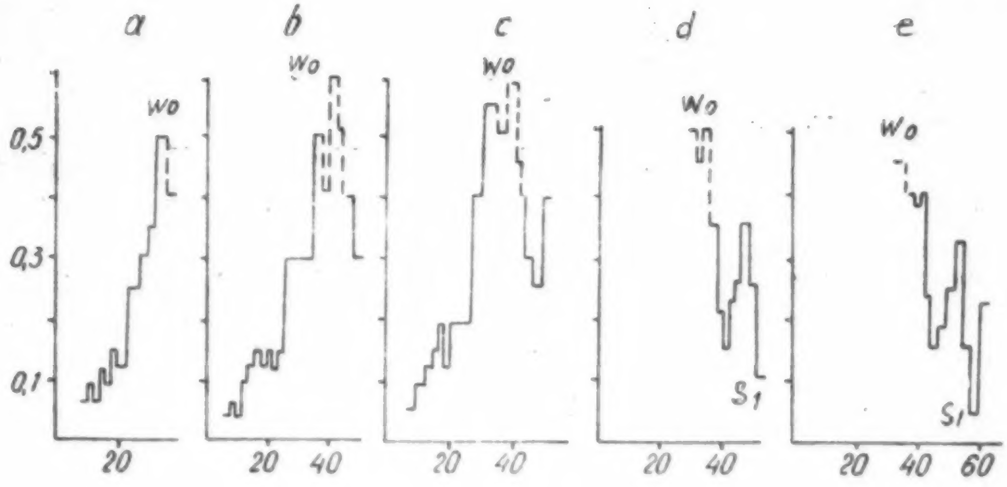


Fig. 44. Seasonal changes in the width of the elementary growth layers of the shell in the Yezo scallop from cages in 1974 (Postovaya inlet of Posyet Bay, Sea of Japan). Periods of formation of final layer of shell: unbroken line - diurnal growth layers; dashed line - elementary growth layers of many days; w - winter, s - summer elementary growth layers of shell. a - 27/III, b - 27/V, c - 5/VII, d - 26/VIII, e - 30/X. X-axis - distance from apex of shell, mm; Y-axis - width of elementary growth layer, mm

When we compare the curves that reflect the seasonal dynamics of the size of the growth layers with the temperature curves plotted on the basis of the ratio of the oxygen isotopes $^{18}O/^{16}O$ (Fig. 41), or when we correlate the linear increments at the margins of the shell, we find that the optimal temperature of linear growth varies between 10 and 14°C for the scallop (Fig. 45). The scatter of dots showing the increment over 24 hours depends on the individual growth characteristics of the mollusks at different ages, random environmental factors, breakage of the shell margins during sampling, sampling errors, and errors of the method. Approximately the same range of temperatures most favorable to linear growth was derived by studying the growth of scallops raised in cages (Tibilova, Bregman, 1975) and by studying this process using the oxygen-isotope method (Ignatyev et al., 1976) and the calcium-magnesium method (Pozdnyakova et al., 1982).

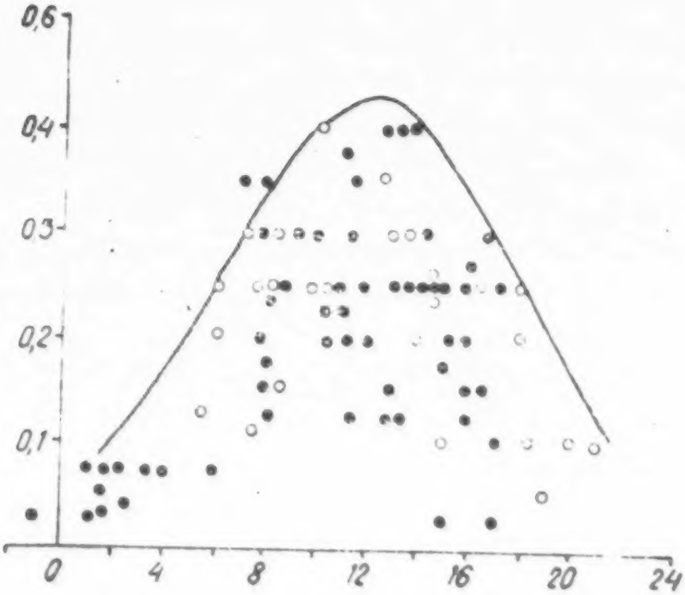


Fig. 45. Changes in linear diurnal increments of the shell in the Yezo scallop from Peter the Great Gulf at different water temperatures. Dark dots - increments and temperature (determined by the method of oxygen-isotope thermometry), light dots - increments at the edges of the shell and the water temperature at the time of sampling. X-axis - temperature, °C; Y-axis - diurnal increment, mm

Of special interest is the curve that rounds the upper series of dots (Fig. 45). It defines the dependence of the shell's growth rate on temperature with the greatest degree of accuracy, and is best described by the function $\mathbf{P(T)=ae^{-b^2(T-T_{opt.})^2}}$, where **P(T)** is the diurnal increment at a temperature of T°C, **a** denotes the maximal diurnal increment for the given species under optimal conditions, and **b** is the constant that characterizes the sensitivity of the mollusk to temperature change. The higher the value of **b**, the narrower the zone of temperature comfort for the animal's growth. By analogy with the normal law of distribution $\frac{1}{b\sqrt{2}} = s$, the range $[T_{opt.} - \frac{1}{b\sqrt{2}}, T_{opt.} + \frac{1}{b\sqrt{2}}]$ represents the optimal temperature zone, where P(T) is the maximum value, or approximates it. According to the results ($\frac{1}{b\sqrt{2}} = 6$; $a = 0.42$ mm/day; $P(T) = 0.42\ 1^{-0.0139(T-12)^2}$), the enveloping curve, calculated by the proposed formula (Fig. 42), clearly illustrates the dependence of the growth rate on temperature.

These results were obtained mainly for 1.5—3-year-old individuals in which the diurnal shell increments were significant and quite discernible. It is difficult to study the effect of water temperature on the linear growth of sexually mature individuals because their growth practically ceases for about 10 days during the spawning period. Perhaps the temperature of linear growth in juvenile scallops, especially at the onset of this stage of development, is higher than in the adults.

The effect of water temperature on the growth rate of the scallop can be both direct and indirect. For example, the solubility of gases in water decreases with an increase in temperature, which can reduce the supply of oxygen to the tissues. Up to the middle of July and from the beginning of October, the oxygen content in Peter the Great Gulf (Vityaz Bay, Furuhelm Is; depth 10 m) is greater than 6 ml/l. During the hottest period of the year, when the rate of linear growth decreases substantially, the concentration of oxygen in the water drops to 5-5.5 ml/l, which is below the optimal level for the scallop (Bregman et al., 1977). A drop in salinity can hardly cause a decrease in the linear growth rate in summer, though the salinity in some areas sometimes drops to 29‰. At the same time, the salinity does not drop below 32.5‰ in the unsheltered areas, e.g. near Furuhelm Is. at a depth of 10 m in July—September, and it is higher than 33‰ during certain years; however, here too, the rate of linear growth slows down in summer.

May—July and September—October are the periods of optimal water temperatures for the growth of the Yezo scallop in Peter the Great Gulf. The increment during the first, lengthier period is slightly smaller than during the second period. This difference is most likely due to the high energy expenditures on the regeneration of genital products in spring.

The decrease in the growth rate of the mollusks in summer is attributed first of all to the decrease in the food supply (Coe, Fox, 1942). However, the slowing of the rate of linear growth and the cessation of gonadal development in July—September in the scallop of Peter the Great Gulf cannot be attributed to the alimentary factor. In the Amur Gulf and Posyet Bay, the biomass of phytoplankton (Konovalova, 1980), bacterioplankton and zooplankton (Karapetyan, 1971) during this period of the year is not less, and the production of plankton (Rassashko, 1974) is even greater than in July and October, when a high growth rate is observed in the scallop. In the opinion of Bregman and coauthors (1977), the growth rate of the scallop depends to a much smaller extent on the content of the seston than on the temperature and oxygen content of the water.

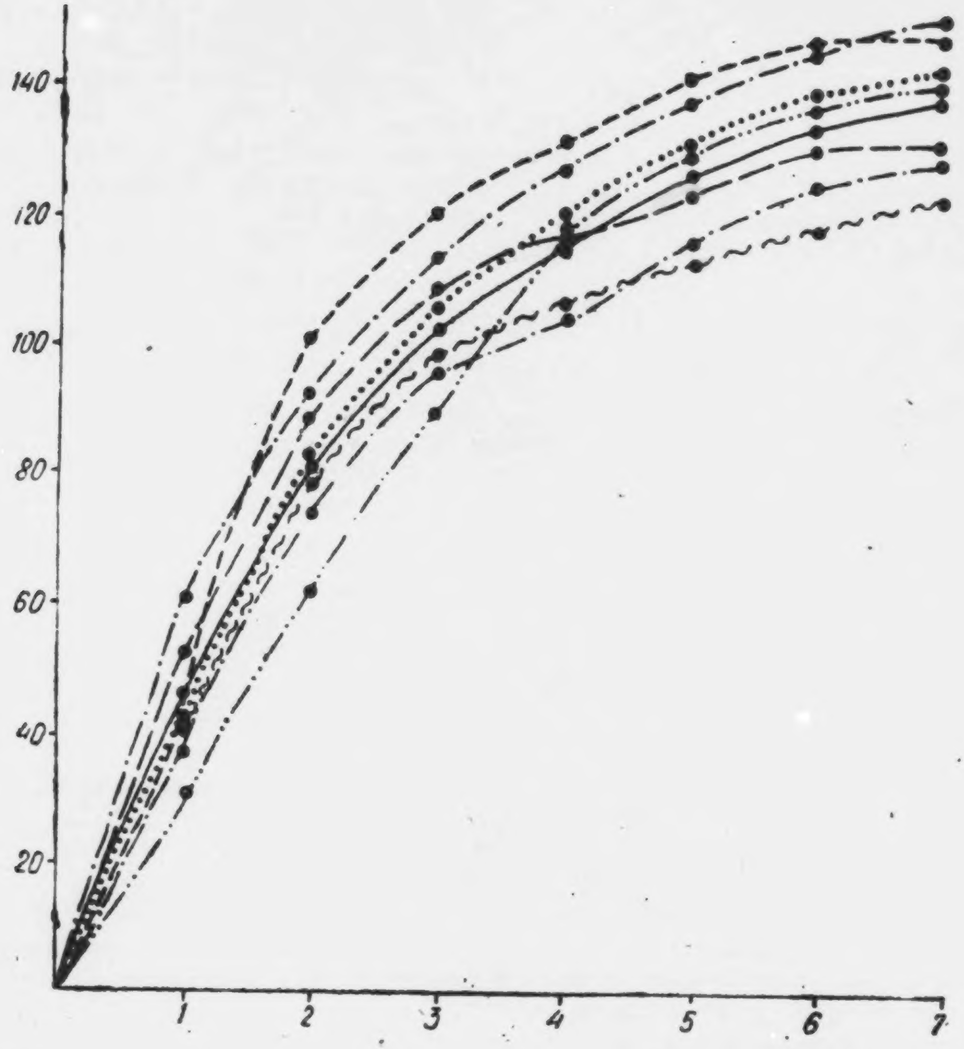


Fig. 46. Growth of individual scallops in 1973, and the mean growth curve (unbroken line) of the whole generation of the Yezo scallop. X-axis - age, yr; Y-axis - height of shell, mm

12.2.5. Individual growth and the growth of individual age groups

The growth of different generations of the scallop differs in the same population; it also differs from the average growth of the population. The growth rate and size of year-old scallops are especially unpredictable; they depend on the conditions in which embryonic and larval development took place.

The coefficient of variation $CV = \frac{sn}{x}$ for all the populations of the scallop decreases significantly with age. For example, the coefficient of variation in Lake Vtoroye of Nakhodka Bay is equal to 16.2% during the first year, 8.1% during the third year, 7.2% during the fifth year, 6.5% during the seventh year, and 4.1% during the eighth year. It also decreases for individual generations, but not as uniformly as for entire populations; sometimes, during particularly unfavorable years, the coefficient of variation may even increase. The shell height variation range is usually the same in scallops of the same age; for example, it constitutes 30 mm in Lake Vtoroye, and remains practically constant for all the ages of the same generation.

It is particularly difficult to predict the growth of an individual scallop, which differs significantly even within the same age group (Fig. 46). Different variants are possible here. A scallop that grows rapidly (slowly) during the first few years later begins to grow more slowly (rapidly). Such changes in growth usually take place with the onset of sexual maturity (Fig. 46). Abrupt decelerations of growth and equally abrupt increases in growth rate are often observed during certain years.

12.2.6. Mathematical description

The changes in the linear size of the Yezo scallop with age are described by the Bertalanffy equation in two modifications. One of these modifications is the formula altered by Vinberg,

$L_t = [L_\infty^{b-a} - (L_\infty^{b-a} - L_0^{b-a}) \cdot e^{(b-a)k(t-t_0)}]^{1/(b-a)}$, where L_t denotes the height of the shell at the age of t years, L_∞ is the definitive height, L_0 is the initial height of the shell, and a, b and k are constants. At the same time, Tibilova and Bregman (1975) and later Mandryka (1979) determined the constant b-a by the values of the exponents in the equation of metabolism (α/β) and the formula of the linear-weight ratio (B) : $b-a = B - \alpha/\beta \cdot B$. Tibilova and Bregman (1975) suggested that equations with different factors be used to determine the linear growth in sexually immature and mature scallops from Troitsy Bay of Posyet Bay. b-a = 0.78 was suggested for the first ones, therefore $L_t = [7.240—6.683 \cdot e^{-0.5915t}]^{1.282}$, and b-a= 1.025 was suggested for the second ones, therefore $L_t = [18.830—10.240 \cdot e^{-0.2450(t-2)}]^{0.975}$. Mandryka (1979) used b-a = 1.025 to determine the relationship between linear growth and age in the populations of the Haloway and Zapadnaya inlets of Posyet Bay, Lake Vtoroye of Nakhodka Bay, and Sokolovskaya Bay of the Olga Gulf.

The Bertalanffy formula is also applied in the form usually used by ichthyologists, i.e. $L_t = L_\infty(1-e^{-k(t-t_0)})$, where L_t and L_∞ denote the same as in the previous variant, t_0 denotes age with $L_t=0$, and k is the constant value. Ignatyev and coauthors (1976) derived $L_\infty=18.7$ and k=0.35 for the Yezo scallop from the Zapadnaya inlet of Posyet Bay.

Silina (1979) recommends using the following factor model to describe the changes in the diurnal increments of the Yezo scallop in relation to environmental changes:

$P_{diur.}=0.4 \cdot \frac{y}{2} \cdot e^{-\frac{y-2}{2}} \cdot e^{-0.0263(T-12)^2} \cdot e^{-0.5(S-33)^2}$ when T >4°C. If $T<4°C$, $P_{diur.}$ is calculated by this formula with T=4°C. During spawning, $P_{diur.}=0$, where $P_{diur.}$ is the diurnal height increment of the shell (mm), y denotes age (yr), T temperature (°C), and S salinity (‰). This model quite adequately reflects the real growth of the shell (Fig. 47).

12.3. Mass increment

The mass of a mollusk is a less stable characteristic than the linear size. It varies significantly from season to season, especially in the sexually mature individuals. The scallop attains its highest mass just before spawning, during the period of maximum gamete maturation. At the same time, the gonads in individuals with a body mass of 404-445 g (in Lake Vtoroye of Nakhoda Bay) attain a mass of 20-57 g, which decreases to 6-10 g after spawning. Therefore, it is possible to compare the mass increment of the scallop in different populations only at the same stage of the reproductive cycle. The mass of the scallop varies for individuals of the same age, and differs significantly in the different generations . For example, sixth-year scallops were found to have a greater mass than seventh-year scallops in Lake Vtoroye, and fifth-year scallops a greater mass than sixth-year scallops in Andreyev Bay (table 29). Some age groups are very scarce or absent altogether in a population, which makes it difficult to study the mass increment of the scallop. Therefore, when studying the mass (W) of a mollusk, we often use averaged values that reflect the dependence of the changes in mass (both total, and of individual organs) on linear size (H) by the formula $W=aH^b$, where a and b are constant values (Fig. 48). The dependence of total mass on shell height usually approximates the cubic mass (table 30), whereas the coefficient for muscle mass in different populations varies to a greater extent (Skalkin, 1966). Conversion of shell height from the mean values to the total mass of the scallop and to the mass of its muscle for each age produces good results which coincide with the mass of a scallop of the same age (compare table 29 with table 30 and also with table 31).

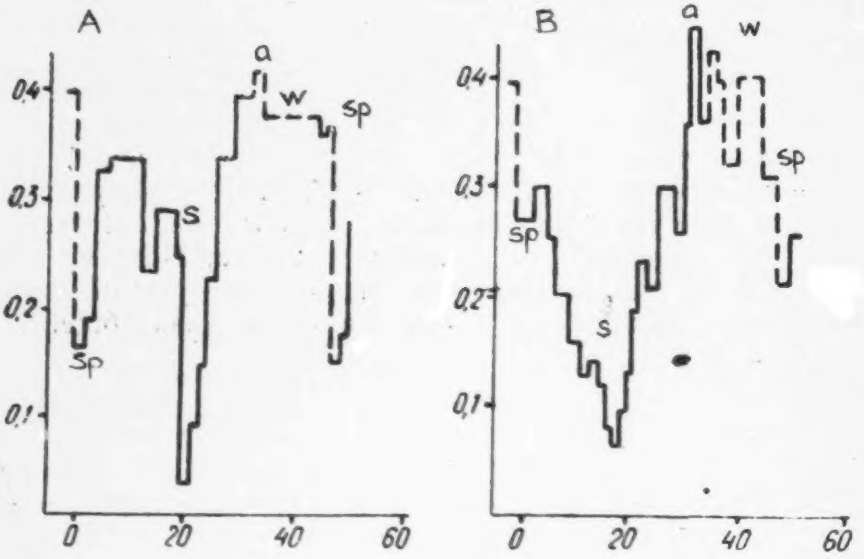


Fig. 47. Calculated (A) and empirical (B) curves of seasonal changes in the width of the growth layers in year-old Yezo scallops during the year in the Zapadnaya inlet of Furuhelm Is. in Posyet Bay of the Sea of Japan at a depth of 10 m. X-axis - width of elementary growth layer (mm), Y-axis - height increment of shell during the year (mm). Dashed line marks winter increments of many days (w), sp - spring transition to diurnal layers, s - summer increments, a - autumn transition to layers formed over a period of many days

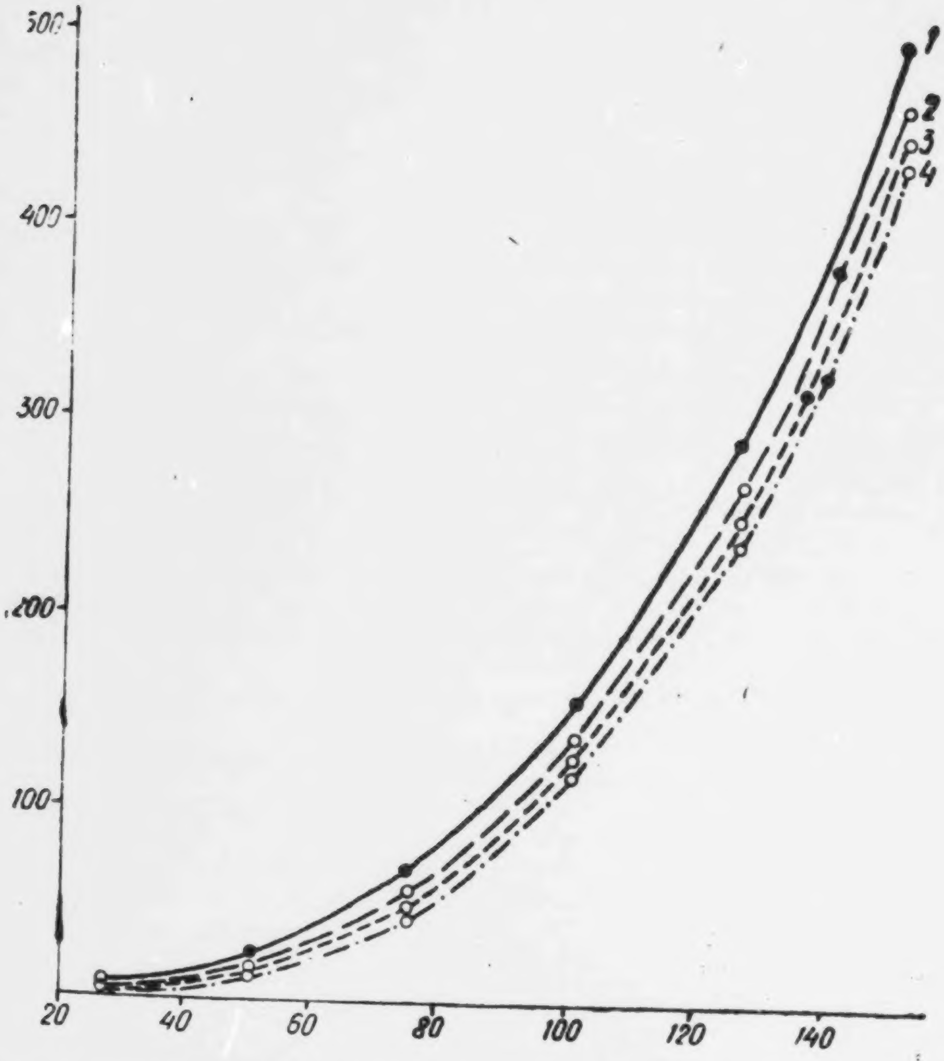


Fig. 48. Changes in the total mass and the shell height of the Yezo scallop from populations inhabiting the waters of 1 - Stenin Is. in Peter the Great Gulf, 2 - Vityaz Bay in Posyet Bay, 3 - Putyatin Is. in Peter the Great Gulf, 4 - Shkot Is. in Ussuri Bay of the Sea of Japan. The total mass was calculated by the formula $W=aH^b$ established for each population separately. Dark dots mark size and weight parameters of 5-year-old scallops, light dots mark those of scallops under 5 years of age. X-axis - total mass of scallop (g), Y-axis - shell height (mm)

Table 29. Mass increment of the Yezo scallop

Age, yr	No. of individuals	Mean value of total mass, g	Mean increment, g
		Lake Vtoroye of Nakhodka Bay	
1	3	2.0±1.1	
2	14	56.4±5.7	54.4
3	32	172.4±6.3	116.0
4	2	282.3±15.6	109.9
5	46	359.6±10.0	77.3
6	56	409.5±9.1	49.9
7	23	367.0±14.4	-42.5
8	20	428.9±13.1	61.9
		Andreyev Bay of Ussuri Bay	
2	14	108.7±3.9	
3	2	183.6±9.3	74.9
4	8	250.4±18.0	66.8
5	3	314.7±30.7	64.3
6	10	272.6±13.6	-42.5
7	10	304.6±9.3	31.4
8	12	326.2±14.6	21.6

12.3.1. Ontogenetic changes

Whereas linear growth in the Yezo scallop proceeds at the highest rate during the first 2-3 years, mass increment is maximal at the age of 2-8 years. At the same time, the periods of highest mass increment of the scallop do not coincide in different parts of its range. In the areas farthest south, a high rate of mass increment is observed in the second—fourth year, and then it slows down considerably with age (Fig. 49). In the northern part of the range, the peak of body mass increment sets in at the age of 4-8 years (Fig.

49). In the populations inhabiting the sheltered and half-sheltered areas of Peter the Great Gulf, the main body mass of the scallop, including its muscle, forms during the second—fourth year; it forms during the second—fifth year in the open and deeper areas (near the Stenin and Furuhelm islands), and during the third—fifth year in the colder areas (the Olga Gulf) (tables 30, 31).

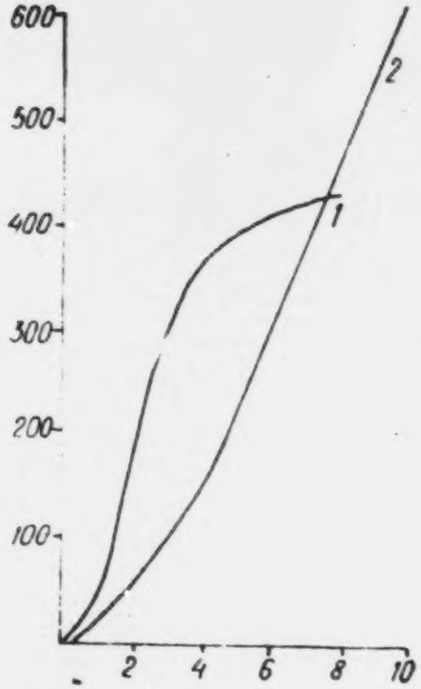


Fig. 49. Weight gain of the Yezo scallop: 1 - in Mutsu Bay, Honshu, Sea of Japan (after Yamamoto, 1964); 2 - in the Busse Lagoon, Aniva Gulf, Sea of Okhotsk (after Kulikova, Tabunkov, 1974). X- axis - age (years), Y-axis - total mass (g)

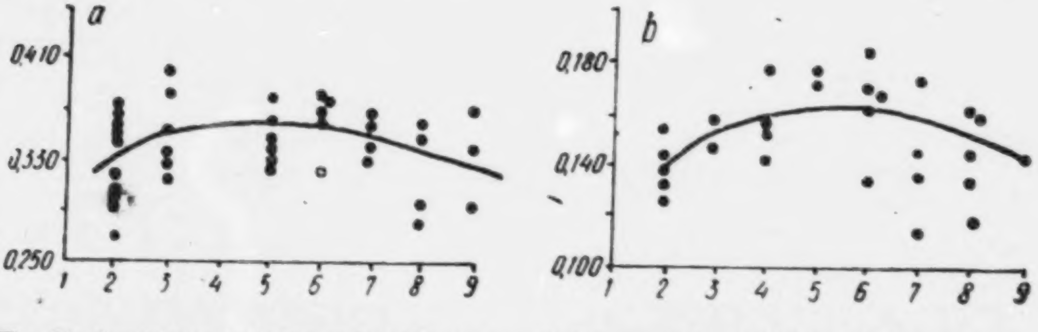


Fig. 50. Age changes in the ratio of the mass of all the soft tissues (a) in Lake Vtoroye of Nakhodka Bay and muscle mass (b) in Andreyev Bay of Ussuri Bay in the Sea of Japan to the total mass of the Yezo scallop. X-axis - values of ratios respectively, Y-axis - age (yr)

Table 30. Ratio of shell height and total mass (g) in Yezo scallops from different populations and the estimated values of total mass based on the average shell height for each age respectively

Area	Condition of gonads	$W_{tot}=aH^b$ W, g; H, mm	Estimated values of total mass of scallop at the age of (yr): 1	2	3	4	5	6
Peter the Great Gulf								
Posyet Gulf								
Ekspeditsiya Bay	Spawning	$0.1718\cdot10^{-3}\cdot H^{2'9404}$	14.5	104.3	202.6	271.8	300.1	-
Vityaz Bay	Prespawning	$0.0990\cdot10^{-3}\cdot H^{3'0656}$	13.2	94.3	212.2	303.6	378.1	425.5
Furuhelm Is.	Prespawning	$0.1270\cdot10^{-3}\cdot H^{2'9992}$	29.3	133.6	247.5	338.9	404.2	482.1
Stenin Is.	Onset of spawning	$0.2823\cdot10^{-3}\cdot H^{2'8687}$	15.2	114.0	261.4	390.9	495.4	580.1
Ussuri Bay								
Priboynaya Bay of Popov Is.	Postspawning	$0.0658\cdot10^{-3}\cdot H^{3'1271}$	14.6	113.1	234.4	319.1	384.2	419.8
Shkot Is.	Postspawning	$0.0541\cdot10^{-3}\cdot H^{3'1686}$	13.9	96.7	190.3	260.3	330.1	381.7
Lazurnaya Bay	Postspawning	$0.0162\cdot10^{-3}\cdot H^{3'4781}$	8.1	69.9	172.2	284.7	346.3	395.6
Putyatin Is.	Postspawning	$0.0435\cdot10^{-3}\cdot H^{3'2249}$	13.7	89.8	194.0	275.1	328.0	372.0
Nakhodka Bay								
Lake Vtoroye	Spawning	$0.1566\cdot10^{-3}\cdot H^{2'9800}$	10.9	75.4	164.2	247.1	316.5	370.5
Melkovodnaya Bay	Spawning	$0.0282\cdot10^{-3}\cdot H^{3'3279}$	8.4	69.2	173.2	301.8	391.2	483.4

Table 31. Ratio of shell height and muscle mass (g) in the Yezo scallop and the calculated values of muscle mass based on the mean shell height for each age respectively

Habitat	$W_{musc}=aH^{b}$ W, g; H, mm	Calculated and measured mean values of mass according to age, yr					
		1	2	3	4	5	6
Peter the Great Gulf							
Posyet Bay							
Ekspeditsiya Bay	$0.219\cdot10^{-3}\cdot H^{2'9700}$	1.8 1.9	15.2 8.2	29.8 19.8	40.1 32.3	44.3 43.9	—
Vityaz Bay	$0.0765\cdot10^{-3}\cdot H^{2'7122}$	2.7 -	15.3 -	31.3 -	43.0 -	52.2 49.0	58.0 59.1
Furuhelm Is.	$0.0327\cdot10^{-3}\cdot H^{2'8977}$	4.9 -	21.4 -	38.9 30.4	52.7 57.2	62.8 -	73.1 74.4
Stenin Is.	$0.7412\cdot10^{-3}\cdot H^{2'2778}$	4.2 -	21.0 -	40.5 -	55.8 -	67.3 -	76.3 -
Ussuri Bay							
Priboynaya Bay of Popov Is.	$1.4136\cdot10^{-3}\cdot H^{2'0930}$	5.3 -	21.1 -	34.3 32.6	42.2 39.5	47.8 49.9	50.7 51.7
Shkot Is.	$0.2546\cdot10^{-3}\cdot H^{2'4678}$	2.7 -	15.6 -	30.3 33.5	40.6 39.9	49.0 48.8	54.9 46.9
Lazurnaya Bay	$0.0900\cdot10^{-3}\cdot H^{2'7029}$	2.4 -	12.9 -	25.9 -	38.4 -	44.7 49.5	49.5 -
Andreyev Bay	$0.7002\cdot10^{-3}\cdot H^{2'2800}$	4.5 -	17.9 15.0	29.7 27.9	37.8 40.2	42.0 -	44.9 45.6
Putyatin Is.	$0.0173\cdot10^{-3}\cdot H^{3'0074}$	2.3 -	13.4 -	27.5 22.4	38.1 39.3	44.8 45.9	50.4 50.6
Nakhodka Bay							
Lake Vtoroye	$0.0087\cdot10^{-3}\cdot H^{3'1855}$	1.3 -	10.3 -	23.7 -	36.7 -	47.9 -	56.6 -
Melkovodnaya Bay	$0.0018\cdot10^{-3}\cdot H^{3'4688}$	0.9 -	8.2 -	21.4 20.0	38.2 27.7	50.1 48.1	61.5 64.5

Note: Numerator - calculated value, denominator - measured mean value of muscle mass

12.3.2. Growth in different populations

As in the case of linear growth, mass increment in the scallops of Peter the Great Gulf is the most intense in the populations found off the Stenin, Furuhelm and Popov islands. In these areas, the total mass of the Yezo scallop and the muscle mass at any age are higher than the same values for the mollusks from the rest of the areas of the gulf (tables 30, 31). Scallops with the same shell height from two different areas have a different mass. Mollusks from populations living close to islands have a higher body mass (Fig. 48) both before and after spawning. The slowest increase in mass is noted in the scallops from the Andreyev Bay and Lake Vtoroye populations.

The threshold parameters of mass are always higher in the scallops from cold-water areas. Particularly extreme differences are observed when comparing the final values of mass increment in scallops from the marginal parts of the range; the mass of a scallop from Mutsu Bay does not usually exceed 500 g, whereas mollusks weighing more than a kilogram are often encountered off the Southern Kuriles (Fig. 49).

12.3.3. Mass ratio of different parts of the body

The proportion of shell mass in the total live mass of the scallop changes insignificantly with age. It usually amounts to more than one-half (52-57%), but increases to 63% in Preobrazheniye and Lazurnaya bays and in the Olga and Terpeniye gulfs (Skalkin, 1966; Bregman, 1979). The ratio of the mass of all the soft tissues of the scallop to its total mass changes significantly depending on the stages of the reproductive cycle; in Peter the Great Gulf, it varies from 30 to 42%, averaging 33% for the area. The value of this ratio increases up to the age of 3 years, remains practically unchanged from age 3 to 6, and then decreases significantly after the age of 7 (Fig. 50).

The mass of the muscle to the total mass varies from 10-12 to 18% for different populations, averaging 14% for the scallop of Peter the Great Gulf; the mass of the muscle to the mass of the soft tissues constitutes at least one-third, and often even 40-45%. The muscle is particularly developed in the scallop populations from the southwestern part of Peter the Great Gulf, and from the Aniva Gulf of Sakhalin Is. The proportion of the muscle in the total mass does not change much with age; it increases up to the age of 3 years, and decreases after the age of 7 (Fig. 50).

13. BEHAVIOR

The movement of the valves forms the basis of the observable behavioral reactions of bivalve mollusks. It is believed that when the valves are open, the mollusk is active (airing the mantle cavity, grazing, breathing) (Salanki, 1965, 1966, 1969, 1973, 1977; Morton, 1969, 1970; Thompson, 1975; Higgins, 1980). Closed valves correspond to an inactive state (no grazing, anaerobic respiratory cycle). Motor activity is regarded as various types of valve movement (movements related to the transition from an active state to a state of rest and back again, aeration and escape responses, etc.) per unit of time.

The members of the Pectinidae, specifically the Yezo scallop, are capable of active migration in their environment by means of the expelled water jet response. This and other aspects of their activity can prove interesting from the point of view of general, evolutionary and applied physiology and ethology. Published data are scarce, sometimes contradictory, and of a descriptive nature (Kalashnikov, 1980; Belogrudov, 1981; Volkov et al., 1982).

Behavior includes all the processes by which the animal reacts to perceived changes in the inside and outside world. The animal can respond to a danger signal by hastily retreating or assuming a different position; it can react with a quickening or slowing of the heartbeat when appearing to be quite inactive on the outside. All of these types of responses are equally regarded as behavior (Karpenko, Dautov, 1976; Kendell, 1980; Libbert, 1982; Dautov, Karpenko, 1983).

13.1. Motor response

The mollusk moves along the bottom by short jumps. The valves of the shell are opened wide; the velum (the muscular outgrowth of the mantle edge) is closed along the entire periphery of the shell, except in the area of the auricles, where openings form. By abruptly contracting the adductor, the scallop forces the valves to close, and the water is expelled through these openings in two strong jets. This reactive force propels the animal ventral side forward (Fig. 51, A). This is how the scallop usually moves. There are also other motor responses related to water expulsion. These include the reaction of jumping aside, in which case an opening is formed in the mantle on the side of the stimulus and the mollusk is propelled in the opposite direction. This type of opening can be formed at any point in the mantle (Fig, 51, B). During the burrowing response, the scallop expels jets of water alternately to the right and to the left of the ligament, building up a screwing motion that buries it into the ground almost to the very edge of the lower (right) valve. The blow-through response pursues the removal of foreign particles and aeration of the mantle cavity (Fig. 51, C). By lightly clapping its valves, the mollusk sends water through the mantle cavity. At the same time, the edges of the velum do not close, and the water is expelled. The burrowing and blow-through responses ensure that the upper valve is covered with sand.

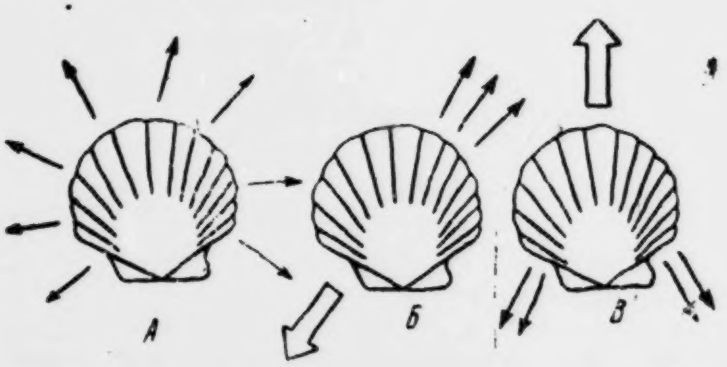


Fig. 51. Motor responses of the Yezo scallop. A - normal swimming; B - retreat response; C - blow-through and aeration response. Small arrows indicate direction of water expulsion, and large arrows the direction in which the animal is moving

To establish the hydrodynamics of "swimming", the scallop was suspended in a specially built measuring mechanotron that made it possible to determine the tractive force exerted during a jump and the change in the position of the animal's centre of gravity. The hydrodynamic profile of the shell was also studied, and the position of the body's force of gravity was determined. The scallop was found to have an asymmetrical profile with a low position of the centre of gravity. Directly before a jump, the centre of gravity shifts due to the posterior displacement of the internal organs (gonad, gills). The anterior margin of the shell jerks slightly upward, and this is immediately followed by the rapid closing of the valves and a jump. At the same time, a small portion of water is deflected by the upper velum downward and to the sides. This mode of jumping lifts the scallop from its burrow. The reciprocal effect of the shifting of the centre of gravity and the downward deflection of the water jet enable the animal to get out of hollows. The ascensional force (buoyancy) of the scallop is ensured by the bevelled anterior margin of the shell when the animal is moving along a flat surface. On the other hand, a low position of the centre of gravity stabilizes the body and prevents the animal from overturning.

The measurement of the specific tractive force (the ratio of the maximum effort exerted by the mollusk at the moment of jumping to its mass in the water) revealed that the specific tractive force changes with an increase in mass. At first, the specific tractive force increases with the mass of the mollusk, but having peaked, it gradually diminishes. The older and heavier individuals are incapable of significant migrations due to a decrease in tractive force. The young scallops not only jump along the bottom, but also swim about in the water, covering up to 70—100 cm in a single "flight", which is 28—40 times greater than the length of their body. A jump of an adult mollusk enables it to cover a distance equal to 2—3 lengths of its body at the most. When swimming, a young scallop claps its valves shut 3—5 times every 2 seconds, whereas adult scallops execute one "clap" in 2.5 seconds at best. It is quite apparent that a young scallop has a higher motor activity than an adult, which is probably due to the greater lability of the adductor muscle and the motor nerve mechanisms of the juveniles (Zhirmunsky et al., 1975; Kovaleva et al., 1982).

13.2. Defensive behavior

The response to escape the predaceous starfish is the best-known one in the Yezo scallop (Karpenko, 1980). The escape response is essentially evoked by an ecologically significant stimulus (the predaceous starfish); therefore, the behavioral act examined in the experiment is a natural one for the animal.

The escape response consists of three successive phases. When at rest, the scallop is found on the bottom, its lower (right) valve buried in the sand. The valves are slightly opened, and the upper and lower margins of the mantle (velum) come together in such a way as to leave two openings (the inhalant and exhalant siphons) between them for the passage of water. The numerous sensory pallial tentacles found along the margins of the velum are retracted and barely visible.

When the starfish *Distolasterias nipon* is 4—7 cm away from the scallop, the latter opens its valves wide, extends the pallial tentacles in all directions, and closes the velum along its entire perimeter. This first stage of the escape response is called the alertness phase. Almost simultaneously with this, the frequency and amplitude of the heartbeat begin to increase by an average 25—30% and 150—200% respectively. Such changes in cardiac activity are characteristic of the escape response alone, and enable us to judge both the onset and development of the response (Karpenko, 1977). The alertness phase lasts 10—20 seconds or more, depending on the speed at which the starfish is approaching. If we were to remove the predator at this time, the scallop would calm down in 15—20 min, the tentacles would be retracted and the valves partly closed, and the rate and amplitude of the heartbeat would return to normal.

The second phase of the escape response is observed 3—10 seconds after the starfish draws close to the scallop (2—0.5 cm), or when the pallial tentacles touch it. The scallop opens its valves even wider, retracts the pallial tentacles, and quickly closes its shell. At the same time, the scallop expels a jet of water through the opening between the halves of the velum, and by the force of a backward thrust, jumps away from the predator (the retreat phase). The specific feature of this phase is that the water is expelled in the direction of the starfish.

The final stage of the escape response (the swimming phase) is basically the scallop's usual mode of migration. When jumping back, the mollusk turns its hinge line toward the starfish; this is followed by a series of rapid "claps" of the valves. Water is expelled in two strong jets on the right of the hinge line, and the mollusk, detaching itself from the bottom for 0.5—2 cm, swims off always ventral side first.

A fresh homogenate from *Distolasterias nipon* will also evoke all the phases of the escape response. Consequently, chemoreception plays a leading role in the organization of the behavioral act in the scallop. The use of a homogenate instead of a live starfish has enabled us to determine the relationship between the response of the scallop and the intensity of the stimulus. A diluted homogenate induces the alertness phase with all of its components, including an increase in the rate and amplitude of the heartbeat. By increasing the concentration of the inductor, we can evoke the retreat phase and the swimming phase in sequence. These experiments have shown that the response itself at each stage of its development is of a reflexive threshold nature, the value of the thresholds increasing from the initial phase to the next.

The escape response is evoked by a specific stimulus. For example, if another species of starfish is used in the experiment (*Patiria pectinifera*), the Yezo scallop does not react even in the case where 3—4 starfish are placed directly on its shell. The rate and amplitude of the heartbeat also remain unchanged in this case. The ability of the scallop to differentiate between predaceous and potentially harmless species of starfish was demonstrated by

Thomas and Gruffydd using *Pecten maximus* as an example (Thomas, Gruffydd, 1971).

The reaction to starfish depends on the age of the scallop. For example, in young scallops (2—4 years old), the reaction is already seen when the starfish is 10—12 cm away from the scallop, and all of the phases occur within 5—15 seconds. The rate of the heartbeat increases by 35—40% in this case. Old scallops (12—14 years old) usually display only the alertness phase, and only when they come into direct contact with the starfish. The rate of their heartbeat does not increase significantly (5—10%). In the case where the ray of *Distolasterias nipon* touches the velum, the scallop forcefully slams shut its valves and with a strong jet of water repulses the predator which usually retreats immediately. The scallop jumps back only after the ray of the starfish has touched its velum several times. These observations lead us to believe that the thresholds of the retreat phases in young scallops are lower than in old ones.

The effect of certain ecologically important environmental factors on the escape response was also tested. With a relatively high water temperature in the aquarium (22—25°C), the escape response in the scallop may be partially or completely suppressed, though other responses, e.g. to touch or darkening, remain normal. The quickening of the heartbeat, even when the starfish ascends on the scallop, proves to be insufficient. Apparently, abiotic environmental factors can in certain cases have a significant effect on the escape response of these mollusks.

The defensive response in the scallop is evoked not only by predaceous starfish. The large predaceous gastropod *Natica* sp. can induce a typical defense reflex in a sexually mature adult scallop. When the foot of the predator comes into contact with the pallial tentacles of the scallop, the latter repels *Natica* sp. with a strong jet of water. As in the case with the starfish, the scallop detects danger at a distance, as evidenced by the change in the rate and amplitude of its heartbeat; however, its reaction to the starfish is stronger than its reaction to *Natica* sp. Perhaps predaceous gastropods do not pose a real danger for an adult scallop. Indirect proof of this is that the scallop actively defends itself against the predator, instead of evading it.

The reaction of the scallop to the starfish is triggered by certain specific chemicals, the nature of which is not known. It is assumed that their action is associated with the destruction of the receptor membrane, or is nonspecific altogether (Zhadan et al., 1980). Because of this, it is worth correlating certain facts (Karpenko, 1981). Steroid glycosides and saponin-like surfactants have been isolated from many species of starfish, sea-urchins and holothurians. It was therefore expected that all the species of sea-urchins would induce the escape response or some of its elements. However, the escape response arises only to the scent of a predaceous starfish or a potentially dangerous object. Moreover, the escape response can be induced several times in the scallop, which is inconsistent with the opinion regarding the disturbance of the receptory properties of the membrane. There are data indicating that some marine invertebrates, including the scallop, are capable of differentiating between a hungry and actively preying starfish from a satiated one, one at rest, or one in poor physiological condition (Philips, 1978). It is clear from this that the question concerning the inductors of the escape response of the Yezo scallop is debatable.

13.3. Acquired forms of behavior

The escape response in the scallop (alertness phase, retreat reaction and swimming reaction) is similar to the unconditioned reflex in the higher animals, since it has its main properties, is stereotypic and stimulus-specific, and is of a threshold nature (Maksimova et al., 1980).

Each stage of development of the starfish escape response is of a reflexive nature, the value of the threshold increasing from the initial phase to the next ones. In addition to the motor components, the starfish escape response also includes a cardiac component, the increase in the rate and amplitude of the heartbeat (Karpenko, 1980). Naturally, the habituation of the escape response, which can develop with repeated introduction of the starfish or with its prolonged presence in the aquarium, involves only the high-threshold phases of the response, but, as a rule, does not apply to the alertness phase or the cardiac component. This enables us to use the appearance of the starfish as a reinforcement when developing a conditioned reaction.

The escape response has a fairly long latent period, from 30 to 60 seconds. The reaction itself develops within one minute on the average; however, it takes 10—15 minutes for the scallop to calm down after the starfish is removed. On the basis of these results, the unconditioned stimulus was produced for two minutes in the process of developing a conditioned reaction, while the intervals between each introduction of the starfish were at least 20 min.

To select the conditioned stimulus, we conducted a special series of experiments, in which the indifference of several ecologically significant stimuli in relation to the escape reaction was tested (tactile stimulation of the mantle, a jet of water directed into the mantle cavity, exposure to diffuse light of 1000 Watts). The mollusks were repeatedly (about 100 times) exposed to these stimuli at different intervals (from 15 seconds to 2 minutes). The results of the experiments have shown that light has the highest indifference level in relation to the starfish escape response, and therefore, it can be used as a signal stimulus. The switching on of a light did not induce a visible reaction in the animals, and the switching off of the light caused the mollusks to close their valves, which differed cardinally from all the phases of the starfish escape response.

The first conditioned responses appeared after 6—10 combinations of switching on a light and lowering a starfish into the aquarium. As the number of exposures to light and the starfish increased, the number of conditioned responses increased, reaching 60% of the total number of escape reactions in the experiment after 80 combinations; however, it did not increase after that, and even decreased somewhat (to 40—50%). A two-day interval after 180 combinations reduced the number of conditioned escape responses to 10—20%, or eliminated them entirely in some mollusks. The given dynamics applies to the escape response of a scallop at the alertness phase. The higher-threshold retreat phase in response to the conditioned stimulus was less common by far (5—10, sometimes 15%). After a 2-day interval, the retreat phase disappeared. Though individual differences were observed in the animals, they did not alter in principle the overall picture of developing a conditioned response.

The changes in the cardiac component of the response were the most objective indicator of the formation of a conditioned starfish escape response to light. With the isolated use of light, the rate and amplitude of the mollusks' heartbeat did not differ from the background ones, whereas after the use of the conditioned-reflex procedure, the rate of the heartbeat increased by 5.5%, and its amplitude by 5—40%.

The developed response weakened after 10 isolated introductions of the conditioned stimulus. Several hours after fading, it spontaneously reappeared in only 5% after the first extinction, and in 8% after the second extinction.

In the control group of scallops with pseudoconditioning after 50 uncombined introductions of the starfish and light, we noted a certain number of responses in the form of the alertness phase (14%) and even the retreat phase (10%), but these responses later disappeared completely after 70 introductions of the stimulus.

These data point to the fact that the time relationship which forms in the scallop as a result of the experimental procedure is unstable in comparison with the conditioned reflexes of other mollusks, specifically gastropods (Litvinov et al., 1976).

13.4. Environmental factors and motor activity

There are very few data on the effect of environmental factors on the behavior and activity of the scallop, and the Yezo scallop has not been studied at all in this respect. The following are the results of original experimental research to establish how the mollusk is affected by temperature, a decrease in salinity, slowly developing hypoxia, the natural photoperiod and synthetic surfacants. Scallops of approximately equal size with a shell height of 145-160 mm were used in the study. After they were caught, the animals were adapted to the conditions of 0.5—1.0 m^3 water-circulating lab aquariums for at least 3 weeks. Gages for recording valve movement were attached to the shell of the mollusks. All the details were worked out to the utmost comfort of the animals; a scallop with this type of gage can apparently live for a very long time. The motor activity, i.e. the number of valve movements per unit of time, was regarded as a criterion of the behavioral responses.

The results of these experiments demonstrated the direct dependence of the motor activity of the Yezo scallop on the temperature of its environment (Fig. 52). The experiments were conducted at different times of the year under the conditions of a flow-through sea aquarium; therefore, the indicated tendencies obviously reflect the seasonal dynamics of the mollusk's motor activity as well. At temperatures approximating zero, the scallop periodically passes from an active state to a state of rest (the valves remain closed for a certain length of time). Short periods of rest lasting from 8 to 15 min were also noted in the majority of experimental animals, except that some individuals closed their valves for 70—120 min. At higher temperatures (6°C, 18°C), only rhythmic valve movements are observed in the scallop; the alternation of periods of activity and rest is not observed. However, other bivalves such as *Anodonta cygnea* (Salanki, Vero, 1969; Salanki,1973, 1977), *Crassostrea virginica* (Galtsoff, 1964; Higgins, 1980; Loosanoff, Nomejko, 1946) and *Lithophaga lithophaga* (Salanki, 1966b) are characterized by periodic transitions from an active state to a state of rest in a wide range of temperatures. The fact that the scallop does not "clap" its valves continuously is apparently due to the functional characteristics of the velum. The inhalant and exhalant siphons of the scallop are formed by the velum near the opercular processes of the shell, but the velum often opens on the ventral surface of the animal as well. Consequently, the velum of the scallop is a highly active structure. Therefore, one can assume that the scallop briefly resorts to the closing of the velum instead of the valves in order to stop filtration and isolate itself from the environment. The behavior of the scallop differs from that of other bivalves when it is exposed to unfavorable environmental factors. Whereas inactive mussels, oysters and *Anodonta* respond to hypoxia, low salinity, pollution and other adverse factors by closing their valves, the scallop displays the escape response or some of its elements (Fig. 53).

Our results have shown that the widespread surfactants in very low concentrations affect the behavior of the Yezo scallop, causing an increase in its motor activity to the extent of the escape response. So far, not much can be said about the mechanism of surfactant action; like other toxic agents, surfactants perhaps affect the animal's specific systems as a natural stimulus (Karpenko, 1974). In the end, such an effect alters the activity of the system by regulating it. It should be said that the monitoring of valve movements in the scallop, as in other bivalves, provides integral information about the animal's total life activity. This method shows great promise in the study of how mollusks are affected by various biotic and abiotic environmental factors, pollutants and biologically active substances.

A diurnal rhythm of motor activity, related to the natural alternation of night and day (the photoperiod), is not noted in the Yezo scallop. There are data indicating that such a rhythm correlated with natural illumination has been established in bivalve mollusks (Salanki, 1966b, 1973; Higgins, 1980), though other authors (Loosanoff, Nomejko, 1946; Galtsoff, 1964) deny its existence.

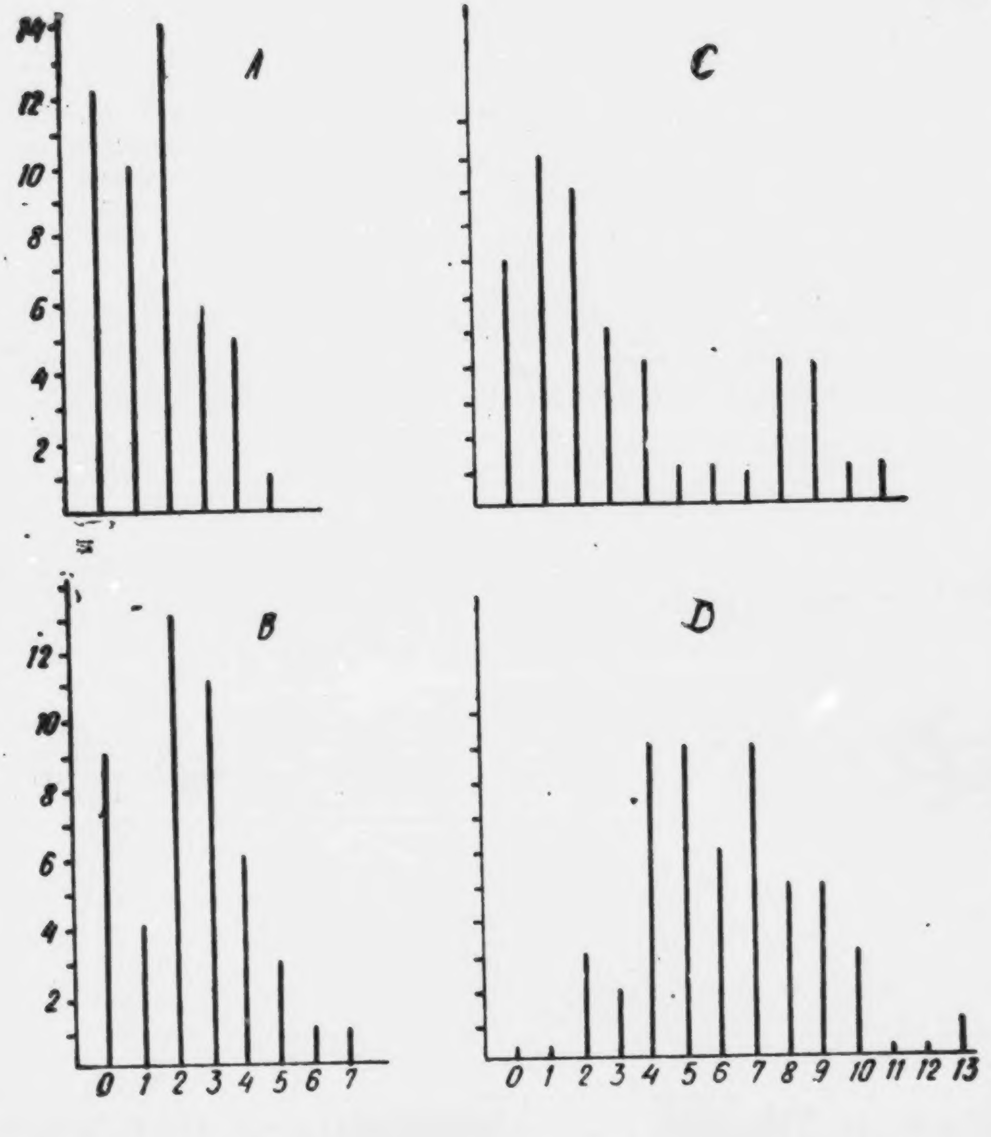


Fig. 52. Effect of temperature on the motor activity of the Yezo scallop. A - 0.2°C; B - 6.7°C; C - periodic temperature fluctuations from 12 to 6.7°C and back; D - 18.5°C. X-axis - number of valve movements in 2 hr; Y-axis - frequency of motor activity levels in 24 hours

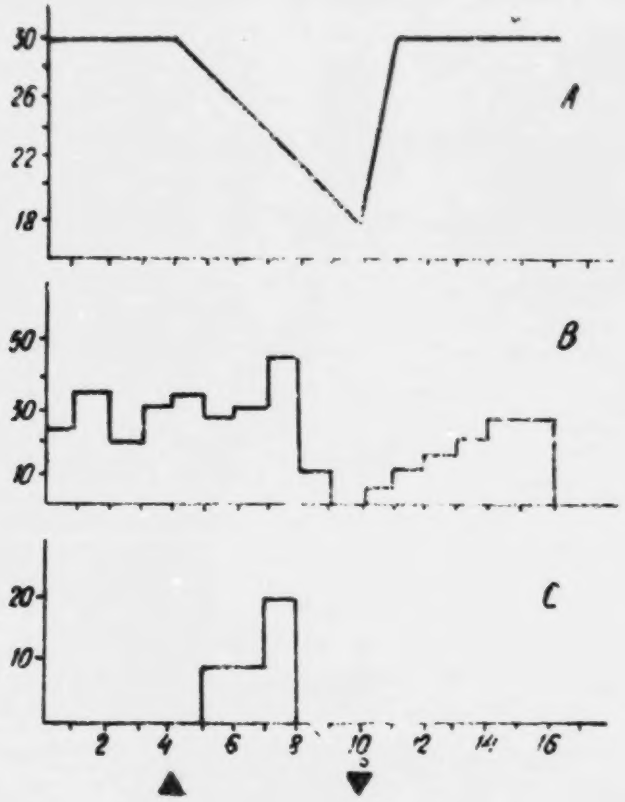


Fig. 53. Effect of a decrease in water salinity on the motor activity of the Yezo scallop. A - salinity dynamics; X-axis in all graphs - time of experiment (one-hour intervals marked); Y-axis - salinity, ‰. B - change in motor activity; Y-axis - total number of valve movements in all experimental animals in one hour. C - escape response (jumps); Y-axis - total number of jumps in one hour. Upward arrow marks beginning of salinity drop; downward arrow marks washing with water of normal salinity.

14. PARASITES AND DISEASES

The Yezo scallop has not been studied very well from the point of view of parasitology. There are a number of reasons why so little information is available on the parasites and diseases of the Yezo scallop. First of all, parasitologists did not pay any special attention to this species for a long time. However, it should be mentioned here that commercial breeding of the scallop began only in 1970 in Japan (Bardach et al., 1978), and even later in the USSR. Secondly, the scarcity of information on the parasites of the scallop reflects the impoverishment of the parasitic fauna and the low degree of infestation of this mollusk. Indeed, the infestation of the Yezo scallop with parasites proved to be very low, its parasitic fauna impoverished, and the latter to contain only potentially pathogenic species of parasites; extensive losses of scallops due to parasitic infestation have never been recorded. Infectious diseases are not known either.

From the available publications, it is practically impossible to establish the total number of Yezo scallops studied so far from the parasitological point of view by previous authors (Okuda, 1937; Buzhinskaya, 1971; Yankovsky, 1973; Stein, 1974, etc.). Judging by the figures given by certain authors, this number is small. During 1972—1982, Tsimbalyuk, Kurochkin, Avdeyev and others of the Animal Parasitology Laboratory of TINRO performed 1341 parasitological dissections of scallops from natural biocoenoses and from maricultural enterprises in Peter the Great Gulf. In 1982, A.V. Rybakov of the Institute of Marine Biology carried out a parasitological study of 110 scallops in Vityaz Bay of the same gulf. These data, published only in part (Avdeyev, 1975; Tsimbalyuk, 1976, 1980; Kurochkin, Tsimbalyuk, 1982; Rybakov, 1983), have been utilized in this section.

Not only the true parasites should be listed among the pathogens that cause this or that infection in the scallop. A number of organisms commonly regarded as commensals can be quite harmful to the scallop, frequently contributing to a specific pathology. There is no doubt that certain commensals, fouling organisms and predators are detrimental to the scallop. The following is a review of the currently known pathogens of the Yezo scallop.

1. *Sirolpidium zoophthorum* Vishniac, 1955

A fungus detected only once in young scallops from Posyet Bay in 1972 has been tentatively assigned to this species. Unfortunately, the material has not been preserved, and we were unable to verify its identification. *S. zoophthorum* is known in the waters off the eastern coast of the USA, where this fungus is the cause of high mortality in oyster spat; it is also encountered in other bivalve mollusks.

2. *Perkinsus* sp. (family Perkinsidae, order Perkins, class Perkinsemorpha, phylum Sporozoa)[2]

At the end of 1979, young Yezo scallops were imported into the USSR from Japan (Aomori Prefecture). After they had been released into one of the inlets of Popov Is., 44 specimens of this scallop were brought to the Laboratory of Marine Animal Parasitology of TINRO for analysis in December 1979. Spherical cysts 0.2—0.3 mm in diameter were found in various organs and tissues in 38 of the scallops (86%). The intensity of infestation was 1—2 cysts. These cysts proved to be trophozoites and prezoosporangia; morphologically, they are very similar to those described for *P. olseni* (see Lester, Davis, 1981). Mature sporangia had long tubes (up to 1.5 diameters of a sporangium), through which numerous very motile flagellate zoospores emerged. Species of the genus *Perkinsus* had never been encountered in the scallop before this.

3. *Pectenita golikowi* Jankowski, 1973 (family Entodiscidae, order Tetrahymenida, class Hymenostomata, phylum Ciliophora)

Endoparasitic infusorians of the species *P. golikowi* were described by Yankovsky (1973) from the intestine of Yezo scallops caught in the sublittoral of the Busse Lagoon; they were also encountered by the same author off Kunashir Is. All of the scallops examined were infested. The intensity of infestation amounted to several tens of infusorians per mollusk. There were no signs of pathogenicity. In our material, infusorians of the species *P. golikowi* were found in scallops from Posyet Bay and the waters off Popov Is. Under normal conditions, they apparently do not cause any perceptible damage to their hosts.

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[2] Nomenclature of higher taxa given after Krylov and Dobrovolsky (1980). Researchers of other countries have assigned the genus *Perkinsus* to the class Perkinsea and the phylum Apicomplexa.

4. *Trichodina pectenis* Stein, 1974 (family Urceolariidae, order Dentodiscida, class Peritricha, phylum Ciliophora)

These ectoparasitic infusorians were described by Stein (1974) from the mantle cavity of the Yezo scallop of Peter the Great Gulf; the same author also found them on the body surface of the sea-urchin *Echinarachnius parma* in the same gulf. In our material, this species of *Trichodina* was encountered in all the areas studied; the extensity of infestation varied from 20 to 100%, and the intensity up to several tens of infusorians. The latter were not found to cause any noticeable damage to the scallop; however, *Trichodina* may play a certain role as secondary parasites in the pathology of the scallop. Actively swimming *Trichodina* often gather in very large numbers on the body of weakened hosts; Tsimbalyuk (1980) has apparently described such a case.

5. *Trichodina* sp. Stein, 1974 (family Urceolariidae, order Dentodiscida, class Peritricha, phylum Ciliophora)

Simultaneously with *T. pectenis* , Stein (1974) discovered several specimens of other, smaller *Trichodina* in the mantle cavity of the scallop; describing them briefly, she assigned them to *Trichodina* sp. Individual specimens of the latter were also found in our material.

6. *Cliona* sp. (family Clionidae, order Hadromerina, class Demospongia, phylum Porifera)

The boring parasitic sponge *Cliona* usually affects the lower valves of the scallop's shell, and comparatively rarely the upper ones (mostly only in large scallops). The galleries bored in the shell by this sponge have a characteristic appearance, branching out like a tree and thinning on the ends. A gallery consists of a chain of fused spherical cavities which hold the body of the sponge; it branches out, but always runs parallel to the inner and the outer surface of the shell within it (Fig. 54). Thin canals, by which the sponge carries out water exchange, extend from each gallery to the outer surface of the shell. Regular rows of small openings on the outer surface of the shell repeat the pattern of all the galleries and branchings within the shell (Fig. 54). From the inner surface of the shell, the galleries of the sponge appear as transparent green (or ocher-yellow when the sponge body dies off) branchlets. They are especially visible when held up to light; this also makes it easier to see the rows of small surface openings that distinguish the galleries of *Cliona* sp. from those of boring polychaetes.

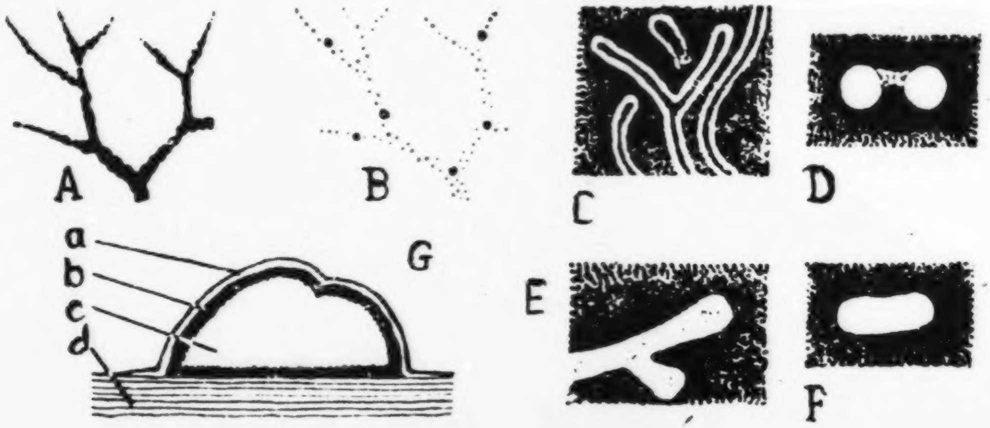


Fig. 54. A damaged scallop shell. A - galleries of boring sponge *Cliona* sp.; B - openings on outer surface of shell along galleries of *Cliona* sp.; C - galleries of polychaetes *Polydora ciliata* and *P. websteri* ; D - transverse section of gallery bored by polychaetes *P. ciliata* and *P. websteri* ; E - galleries of polychaete *Dodecaceria concharum* ; F - transverse section of gallery bored by *D. concharum* ; G - form of blister: a - thin layer of lime forming blister, b - soft organic layer lining inside of blister, c - cavity of blister filled with seawater, d - calcareous layers of scallop shell

Cliona sp. apparently tries to extend thin canals from the main galleries onto the inner surface of the scallop's shell; however, secreting additional calcareous layers, the mollusk does not permit the formation of openings here; in any case, on the inner surface of the shell above the transparent galleries of *Cliona* sp., we usually note convexities that repeat the pattern of the galleries.

The width of the *Cliona* galleries in the shell of the Yezo scallop usually varies from 0.7 to 1.4 mm; the diameter of the ostia on the outer surface of the shell measures 0.23—0.33 mm, and the distance between adjacent ostia in a row is 0.55—0.75 mm; in the same row, the ostia are usually of the same size, but larger ones measuring 0.55—0.76 mm in diameter are sometimes encountered among them.

The lesions caused in the Yezo scallop by *Cliona* , the species of which has not yet been identified, are very similar to those caused by *Cliona vastifica* in *Placopecten magellanicus* (Evans, 1969); however, the *Cliona* galleries in our case are green instead of yellow. We have not come across any information in the literature that boring sponges have been found in the Yezo scallop, though they have been encountered in *Crenomytilus grayanus* in Peter the Great Gulf (Gerasimov, 1979). In our material, we noted that up to 70% of the lower valves of the scallop and up to 10% of the upper valves were affected by *Cliona* sp. in some areas.

7. *Podocotyle* spp. (family Opecoelidae, order Fasciolidida, class Trematoda, phylum Plathelminthes)

Various tissues of the scallop (including the adductor muscle) from Posyet and Vostok bays were found to contain trematode metacercariae which were morphologically similar to the metacercariae of *Podocotyle* species; they were most likely assigned to this genus (Tsimbalyuk, 1976; Rybakov, 1983), though amphipods, not mollusks, are the normal supplementary hosts of *Podocotyle* spp. Metacercariae were encountered in 13 scallops (0.9% of all the scallops analyzed), always one per host. They were encased in a thin, completely transparent cyst with a very soft membrane.

Our largest specimen measured 274 µm in the diameter of the cyst, and 446x103 µm in the body of the metacercaria. The oral sucker measured 43 µm in cross-section, and the ventral one 121x86 µm.

8. *Polydora ciliata* (Johnston, 1838) (family Spionidae, order Spiomorpha, class Polychaeta, phylum Annelida)

This widespread species of polychaetous worms has long been known for its ability to pierce the shells of various mollusks (Soderstrom, 1923; Medcof, 1946; Dorsett, 1961; Blake, Evans, 1973; etc.). Okuda was the first to note *P. ciliata* in the shell of the Yezo scallop off the northern shores of Hokkaido (Okuda, 1937). However, this species is one of the most common borers of Yezo scallop shells, and has been noted many times after that, particularly in the waters of Primorye (Maritime Territory of the USSR) (Kurochkin, Tsimbalyuk, 1982; etc.); the polychaetes found here have been described as the local subspecies *P. ciliata possjetica* Buzhinskaya, 1971 (Buzhinskaya, 1971). Our specimens were also assigned to the subspecies *P. ciliata possjetica* (identification checked by Tarakanova, Institute of Marine Biology). The upper (left) valves are affected the most. Our surveys have shown that the extensity of infestation of adult scallops by these polychaetes reaches 75%. However, galleries bored by different species of polychaetes are usually found in the valves at the same time; furthermore, the empty galleries of same species of polychaetes are often occupied by other species of polychaetes, which makes it very difficult to determine how many lesions were caused by certain species of polychaetes.

P. ciliata bores double galleries (Fig. 54) which branch out, but apparently never intersect; they open in pairs of openings always on the outer surface of the scallop shell. Galleries of this type have been described for a number of species of boring polychaetes. Polychaetes sometimes utilize old *Cliona* galleries, expanding them as they do so. *P. ciliata possjetica* have also been encountered in the cavity of some blisters, but it is difficult to say whether they had anything to do with the formation of these blisters.

9. *Polydora websteri* Hartmann, 1943 (family Spionidae, order Spiomorpha, class Polychaeta, phylum Annelida)

Shell lesions caused by polychaetes of the species *P. websteri* in various bivalves have been described time and again (Turner, Hanks, 1959; Evans, 1969; Zottoli, Carriker, 1974, and others); they have also been noted in the Yezo scallop (Kurochkin, Tsimbalyuk, 1982). These polychaetes are common in the Yezo scallop of Peter the Great Gulf; however, the galleries bored by them in the shell of the scallop (Fig. 54) are very similar to those of *P. ciliata* (Zottoli, Carriker, 1974), therefore it is impossible to count the numbers of either of these species of polychaetes by their galleries. *P. websteri* are sometimes found in the blisters, in some cases together with *P. ciliata* .

10. *Dodecaceria concharum* Oersted (family Cerratulidae, order Spiomorpha, class Polychaeta, phylum Annelida)

The boring polychaete *D. concharum* builds wider galleries than *P. ciliata* . The galleries are single ones and flattened in cross-section (Fig. 54). The blind ends of the galleries are often highly expanded (Fig. 54). This species utilizes the old galleries of other polychaetes or *Cliona* sponges by widening and continuing them. *D.*

concharum is previously known from Posyet Bay (Buzhinskaya, 1971), but it was not noted in scallop shells there.

11. *Herrmannella longicaudata* G. Avdeev, 1975 (family Sabelliphillidae, order Copepoda, class Crustacea, phylum Arthropoda)

These small (1.9—2.2 mm long) cyclopoid copepods have been found in *Mizuhopecten yessoensis* and *Swiftopecten swifti* of Posyet Bay (Avdeyev, 1975). In the waters of Primorye (Maritime Territory of the USSR), they are encountered everywhere (found in the mantle cavity of up to 70% of the Yezo scallops examined); they are apparently commensals, for even in the case of a high degree of infestation, no pathological symptoms have been noted in the scallop. Copepods of the species *H. longicaudata* are fast swimmers, they can freely leave the mantle cavity of the scallop and return to it. They were at one time mistakenly identified as *Modiolicola bifida* in the Yezo scallop (Tsimbalyuk, 1976).

12. *Odostomia fujitanii* Yokogawa, 1927 (family Turbonillidae, order Heterostropha, class Gastropoda, phylum Mollusca)

These small (maximum shell height 5 mm) littoral gastropods often attach to various bivalve mollusks, feeding on them as temporary parasites with the help of their long proboscis which they insert between the valves of the host mollusk. *O. fujitanii* are frequently noted on the Yezo scallop.

The polychaetes *Polydora uschakovi* (Kurochkin, Tsinbalyuk, 1982), *Polydora* cf. *socialis* , *Exogone gemmifera* , *E. olegi* , *Nereis tigrina* , etc. have repeatedly been found in the galleries of borers; all of these species are apparently the secondary dwellers of these galleries. Some authors indicate that the young of the bivalve mollusk *Hiatella arctica* can perforate the shells of larger mollusks, and expand the galleries existing in them. We have seen individual *H. arctica* on the shells of the Yezo scallop, but did not note any boring activity on their part. Various free-living copepods of the suborders Harpacticoida and Cyclopoida (genera *Tisbe* , *Porcellidium* , etc.) can often be encountered in the mantle cavity of the Yezo scallop. They undoubtedly occupy the mantle cavity only temporarily and for a very short time; naturally, they cannot be regarded as pathogenic for the Yezo scallop either.

Though the list of the Yezo scallop pathogens recorded by us includes 12 species, only a few of them can be potentially harmful to this mollusk. The parasitic fungus *Sirolpidium zoophthorum* and sporozoan *Perkinsus* sp. could be the most dangerous ones; however, they were each encountered only once.

The metacercariae of the genus *Podocotyle* are rarely encountered, and apparently are not pathogenic for the scallop. None of the three infusorians noted, nor the copepod *H. longicaudata* are highly pathogenic. It is also very unlikely that the parasitic gastropod *O. fujitanii* could cause much harm. That leaves only the parasites that inhabit the shell of the scallop, the *Cliona* sponge and the four species of polychaetes which, as we know, do not feed off their host and are not usually classed as parasitic organisms. Nevertheless, they are apparently the major pathogens of the scallop.

As a rule, borers of several species are encountered in the shells of adult scallops. The number of galleries gradually increases, and very often old galleries are expanded not only by their own "builders", but also by polychaetes of other species. Various non-boring polychaetes and other invertebrates often occupy the free galleries. With time, the repeatedly perforated shell becomes brittle and, as shown in mussels (Kent, 1981), more accessible to various predators. The galleries directed toward the inner surface of the shell are continuously closed by the mollusk with new layers of lime. As a result, the inner surface of the shell becomes bumpy, and the valve itself can become much thicker and heavier. The thickness of the upper valve sometimes increases 3—4-fold, often very nonuniformly. The much heavier shell makes swimming more difficult for the scallop, and this makes the latter more accessible to starfish and other predators.

In some cases, so-called blisters (from 1.5 to 4 cm in cross-section and up to 1—1.5 cm high) form on the inner surface of the shell, usually on its upper valve; they are composed of a thin layer of lime, and have a large single cavity which opens on the outer surface of the shell in one or two ostia and is filled with seawater and detritus (Figs. 54, 55). The cavity of the blister is lined with a relatively durable dark-brown thick film which usually shows through the layers of lime. Various polychaetes are often found in the blisters. We do not know how these blisters are formed, though the relationship with polychaetes was noted more than 300 years ago in oysters.

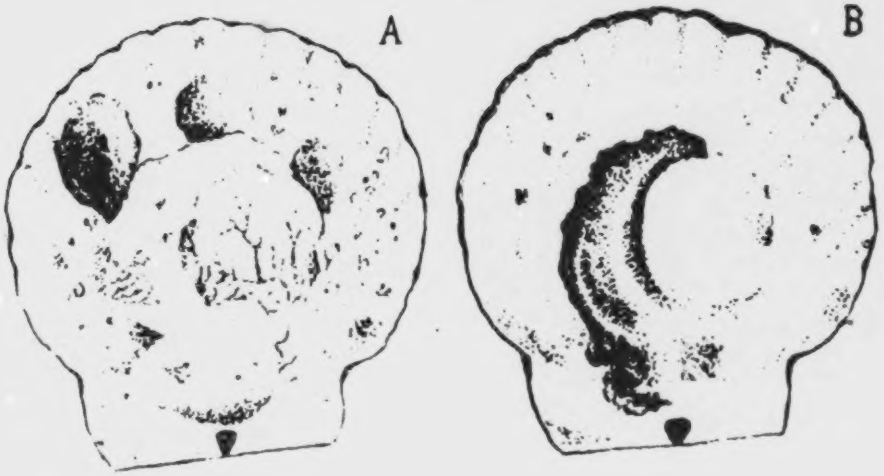


Fig. 55. Position and form of blisters on the upper valve of the Yezo scallop. A - blister of the usual type, B - blister that repeats the form and position of the gonad

In the Yezo scallop, blisters are most commonly located near the edges of the upper valve. There is a special type of blister, which is very large, located above the gonad, and repeats the form of the gonad exactly (Fig. 55). The mechanism by which such blisters are formed apparently differs somewhat from that of the usual type. Blisters and thickenings of the shell can greatly reduce the volume of the space between the valves of the scallop, squeezing its body. However, the major factor is that the accelerated shell secretion stimulated by the activity of *Cliona* sp. and polychaetes requires additonal energy, which exhausts and weakens the mollusk. For example, it was shown in *Mytilus edulis* (Kent, 1979) that a high degree of shell infestation with *Polydora ciliata* results in a lower condition index.

Boring polychaetes are not obligate symbionts of mollusks. It is believed they feed on detritus, and build their tubes in muddy substrates in large numbers. The valves of Yezo scallops living on muddy substrates are infested to a higher degree than in those inhabiting a rocky substrate. In the Yezo scallop, polychaetes prefer to occupy the upper valve, while *Cliona* sponges prefer the lower one. The overall infestation of the upper valves in an adult scallop is usually much higher than in the lower ones. The extensity of their invasion is usually several times (up to 15, most commonly 3—5 times) higher, and the intensity of infestation is also substantially higher.

The scale of overall infestation of Yezo scallop shells was quite extensive. 100% of the shells in adult scallops were affected at many points along the coast of Peter the Great Gulf. Highly infested shells with thickened valves (up to 40%), a multitude of galleries and blisters (up to 25%) are frequently encountered. On the other hand, accumulations of almost intact scallops can be found in some areas.

Kurochkin and Tsimbalyuk (1982) got the rare opportunity to compare the changes in the degree of invasion of Yezo scallop shells by borers over long periods of time. In one of the inlets of the Krabbe Peninsula (Peter the Great Gulf), we found a large accumulation of shells (over 80 m in length, about 25 m in width and up to 2.5 m in height) left over from the harvesting of scallops (from about 1900 to 1950). A bore pit was dug in the central part of this accumulation, and from it we took samples of 500 scallop valves from each of the three layers dating back to about 1900—1910, 1920—1930 and 1940—1950 respectively. Five hundred valves from the present-day scallop of the same bay (1975) were also examined. On the Peschanyy Peninsula, we also examined 25 scallop valves from the Neolithic shell heap dated VII—V century B.C., i.e. the scallops were harvested about 2500 years ago (see Okladnikov, 1959). A comparison of the extensity of invasion of the upper (left) valves showed individual slight lesions in the VII—V century B.C., 52% invasion in 1900—1910, 56% in 1920—1930, 58% in 1940—1950, and 94% invasion in 1975. The intensity of invasion of the lower (right) valves of the scallop also increased from an altogether insignificant level to 81% in 1975 (Kurochkin, Tsimbalyuk, 1982). The causes of the increase in the infestation of scallop shells with boring polychaetes are still unknown.

The literature indicates that *Cliona* sponges can destroy the mollusk, and then continue to destroy its shell. Judging by the material available to us, the *Cliona* sponge encountered in the Yezo scallop does not do this. However, the pathogenic role of borers is unquestionable. Another characteristic feature is that polychaetes perforate the shells of only live scallops, inflict the injuries specific for each species, and cause specific response reactions in the host organism. This prompts us to regard the interrelations between the mollusks and the parasites perforating their shells as "classic" parasitism, or at least one of its little-researched forms. In any case, this phenomenon does not fit into the framework of commensalism or any other known types of symbiosis (with the exception of parasitism).

The formation of a pearl is another manifestation of pathogenesis in bivalve mollusks. It is common knowledge that in the cases where a foreign object lodges under the mantle and does not attach to the surface of the shell, it is gradually coated with concentric layers of lime, and becomes a continuously growing pearl. Pearls form around grains of sand and other hard particles, as well as dead parasites.

In the cases where the pearls encountered in the shell of a Yezo scallop are of parasitic origin, they are most likely formed around dead copepods of the species *Herrmannella longicaudata* . These small, active and most prolific parasites of the Yezo scallop can lodge under the mantle of the mollusk, where they can, apparently even after death, remain attached to the soft tissues of the mantle with the help of a long posteriorly recurved chitinous beak formed by the terminal part of the rostrum. Our thin sections of several pearls have confirmed this assumption. The largest pearls found in the shells of the Yezo scallop had a diameter of up to 5 mm, but they are mostly 1—2 mm in diameter. This pearl is usually irregular in form, and does not have the lustre characteristic of pearls.

Therefore, though the research into the parasitic fauna of the Yezo scallop is very far from complete, we can still say that, compared with many other groups and species of marine mollusks (including commercially important ones), the Yezo scallop has a relatively impoverished parasitic fauna and should be regarded as quite safe from the epizootiological point of view. Indeed, of the 12 species of pathogens recorded in the Yezo scallop, 4 species are shell-boring organisms; of the remaining 8 species that can be regarded as true parasites, 2 species have been encountered only once, one species (metacercariae of trematodes) is encountered very rarely, and the other 5 species (infusorians, copepods and gastropods) do not cause any significant pathology in the scallop under normal conditions. The Yezo scallop is not parasitized by any species that could be harmful to man.

15. PREDATORS

At different stages of its life cycle, the Yezo scallop is exposed to the negative effect of a number of organisms. A vast number of its larvae are eaten up by various seston-eating invertebrates and fishes. After the transition to the benthic mode of life, the mollusks are destroyed by some of the animals that settle on their valves, primarily perforators (polychaetes, boring sponges, bivalve mollusks). A smaller number of scallops is destroyed as a result of uplifting from the bottom by fouling algae, the buoyancy of which is greater than the mass of the scallop (Skarlato, 1960; Belogrudov, 1981), and by ascidians that prevent the scallop from opening its valves (Zhyubikas, 1969), etc. This section examines how metamorphosed scallops are affected by predators, large active animals that feed on mollusks.

15.1. Starfish

The majority of authors regards starfish as the major enemies of the scallop. Though the literature deals extensively with the feeding of starfish on bivalve mollusks (Sloan, 1980; Jangoux, 1982), data on the scallop as a food of starfish are quite scarce and not always reliable. Some authors claim that starfish are the main cause of scallop mortality (Yamamoto, 1964; Biryulina, 1972b). For example, Biryulina reports that starfish destroy up to 50% of the scallop stocks of Peter the Great Gulf annually. However, this opinion is based entirely on the assumption that "mollusks comprise 0.1 of the food consumed by starfish, and the latter feed equally on scallops, mussels, *Modiolus* and *Spisula* " (Biryulina, 1972b, p. 49). The author absolutely ignores both the real ratios of food organisms consumed by the starfish, and their order of preference by the latter; therefore, the given estimate obviously cannot be taken into account.

A series of experiments and observations has shown that the intensity with which starfish feed on scallops depends largely on the age of the mollusks and the availability of other food organisms.

Most of the data on the grazing of scallop spat by starfish were obtained during the biotechnological development of scallop farming. Starfish of the species *Asterias amurensis* spawn nearly at the same time as the scallop; therefore, the starfish larvae settle on the collectors of scallop larvae almost at the same time as the latter. According to Konovalova and Polikarpova (1983), the average number of scallops and starfish found on the sea collectors in Posyet Bay during different years amounted to (specimens per collector):

	1976	1977	1978	1979	1981	1982
Scallop spat	550	450	151	503	323	161
Starfish	0.5	10.0	—	3.3	0.5	—

Prior to 30 September 1977, the mortality of the scallop amounted to 61% during substantial settling of starfish, and did not exceed 2% in the absence of starfish. During that same year, starfish destroyed 26—60% of the scallop spat on the collectors in Minonosok Bay, and 37—100% of the scallop spat near Ivanov Bank (Belogrudov, 1981). By September—October in 1978, the starfish had destroyed 24.6±21.8% of all the scallops on the collectors (Gabayev, 1981). The starfish attacked only mollusks younger than themselves, or of the same age; scallops one year older than the starfish were not consumed by the latter.

Starfish also cause considerable damage to the young of the Yezo scallop under suspended culture. Anayama and coauthors report that even 2—3 starfish in a suspended holding net can destroy 500—800 scallops measuring 5—10 mm and more (Anayama et al., 1974—1975).

The significance of the Yezo scallop as a food of starfish has been studied in Sunahara Bay, Hokkaido (Arima et al., 1971). Scallops were found in the stomachs of starfish only in July and August, when the young of this species pass over to a benthic mode of life. In July, the young of the scallop were found in the stomachs of 17.1% of the *A. amurensis* , 18.2% of the *Distolasterias nipon* and 1.1% of the *Patiria pectinifera* , and in August in 3.2, 8.3 and 1.7% of these species of starfish respectively. The number of scallops found in the stomach of one starfish amounted to 1.4—2.2 in *A. amurensis* , 1.5—4.5 in *D. nipon* , and 1 scallop in *P. pectinifera* . In July, the size of the Yezo scallop shells in the stomachs of the starfish approximated the size of the shells on the adjacent parts of the sea bottom; in August, the starfish consumed the mollusks which were smaller than the modal size of the scallop in the sea. In October, the scallop was not grazed by starfish. In the opinion of the Japanese researchers, the size of the scallop during this period (2.63±0.29 cm) is the maximum one for starfish.

Arima (1973) conducted observations of starfish behavior for 3 days after 10,000 juveniles of the Yezo scallop were released onto the sea bottom. He reports that it is easier for starfish to detect an accumulation of mollusks if it is located upstream. The sensitivity of the starfish is also influenced by the size and density of the concentration.

A large-scale experimental study of the interrelations between the young of the Yezo scallop and starfish on the sea bottom was carried out in Vityaz Bay of the Sea of Japn (Volkov et al., 1982). Approximately 500,000 one-year-old scallops were released in three marked-out study areas.

In the course of the observations later carried out by sea divers, it was noted that the starfish had relocated directly to the place where the scallops were released and the adjacent areas. The configuration of the high-density fields of *A. amurensis* , *Distolasterias nipon* and *Patiria pectinifera* corresponded to that of the scallop. A high density of *Distolasterias nipon* (1—12 specimens/m^2) was observed in the areas where the young of the scallops were first released. With the redistribution of the mollusks, the accumulations of *Distolasterias nipon* shifted subsequent to the shift in the density peaks of the scallop population, but with some delay. The distribution of *A. amurensis* changed in a similar manner, but the picture was less obvious because of the much smaller numbers of this species in the study area.

In the course of the experiment, intensive grazing of scallop juveniles by starfish was observed. Unfortunately, it was not possible to determine what proportion of the dead mollusks was due to predation by starfish, rather than to weakening of the animals in the course of transportation to the study areas. It should be said that the density of stocking in the given experiment was higher by three orders of magnitude as compared with the density observed under natural conditions, which undoubtedly increased the estimate of the losses inflicted by the starfish.

During the summer of 1983, Kalashnikov studied the survival rate of juvenile scallops after they were transplanted to a substrate at the commercial plantation in Posyet Bay. The 200x25 m plantation was located on a sandy bottom at a depth of 12—13 m about 50 m from a rocky shore. The planting of 180,000 one-year-old scallops was carried out on May 12th at an estimated initial rate of 36 specimens/m^2. Subsequent counts taken by divers showed that the abundance of live scallops steadily decreased. The number of empty valves at first increased, and then began to diminish.

Of the large species of starfish in the area, we noted only *D. nipon* (length of ray 12—30 cm) with a background density of 0.48 specimens/m^2. The count taken 2 weeks after the transplantation of the scallops showed that the number of starfish remained practically unchanged; after another ten days, their abundance in the area almost doubled to 0.87 specimens/m^2. The abundance of starfish later decreased to values much lower than the initial ones.

The decrease in the abundance of the scallop and *Distolasterias nipon* in the study area was determined largely by the intensive wave action which caused the shoreward displacement of the mollusks. On May 26th, a tsunami wave entered the bay, resulting in the destruction of the plantation. However, there is no doubt that starfish play a major role in the destruction of the scallop. As the starfish became concentrated in the study area, the proportion of starfish feeding on scallops increased to 75%. During the period of intensive grazing, *D. nipon* attacked the scallop almost continuously. However, the scallop usually dodged the starfish approaching it. The capture of a young scallop by a starfish was very rarely observed, which indicates that this is quite a formidable task even for an active predator like *Distolasterias nipon* .

Kim (1969a) carried out a quantitative study of the size selectiveness of scallop grazing by starfish. *A. amurensis* of three size groups were used in the experiments, i.e. large (length of ray 121 mm), medium (83 mm) and small (53 mm). The minimum size of the scallop was 20 mm, and its maximum size was about 1.5 times greater that the length of the ray in the corresponding size groups of starfish.

The large and medium starfish selected mostly 40—50 and 20—40 mm scallops respectively; at the same time, the selectiveness of these starfish diminished in the direction of both the large and the small mollusks. Small starfish selected mostly the smallest scallops (20—30 mm). The experiments showed that the largest shell from the scallops utilized by starfish of the large, medium and small size groups measured 80, 70 and 30 mm respectively, i.e. the size of the mollusks consumed by the starfish did not exceed 70% of the radius of the latter.

The differences in the harmfulness of starfish to scallops of different size are confirmed by the fact that the mollusks react differently to the approach of these predators; the reaction in young individuals (4—6 cm) is much stronger (Karpenko, 1980, 1981).

The attractiveness of the scallop as a food object in comparison with other mollusks is an interesting question. Kim determined the quantitative feeding selectiveness of *A. amurensis* under experimental conditions (Kim, 1969a). The indices of electiveness, preference and availability were determined (after Ivlev, 1955). *Mizuhopecten yessoensis* , *Mytilus edulis* , *Scapharca broughtoni* , *Tapes japonica* and *Crassostrea gigas* of the sizes most preferred by starfish were used as the food objects. The Yezo scallop proved to be the least attractive to the starfish; its index of electiveness was the lowest (—0.33±0.01), and the index of preference nonexistent (–1.00±0). In Kim's opinion, based on the results of the described experiments, starfish of the species *A. amurensis* cannot be regarded as enemies of the Yezo scallop if other species of bivalve mollusks live alongside it. We obtained similar results for *D. nipon* . Kim attempted to correlate his own results on the feeding selectiveness of starfish with the effort exerted by them to open the valves of the above-mentioned five species of mollusks (Kim, 1969b). We found that the time required for the starfish to open the valves in four of the species was inversely proportional to the index of preference. The Yezo scallop was an exception; its valves were opened in the shortest period of time (about 2.5 hours). To explain this inconsistency, the researcher compared the kymograms characterizing the movement of the valves as they were being opened by the starfish. The kymogram of the Yezo scallop differed considerably from those of the other species of mollusks; the valve movements were stronger and more frequent, the most active movements being noted at the onset of the attack and during the penetration of the ventricle between the valves. Kim believes that this type of reaction on the part of the scallop is an obstacle for the attacker, which explains the low index of preference.

The reaction of the Yezo scallop to an approaching starfish varies with the species of the latter. The escape reaction of the scallop to the starfish *D. nipon* is less manifest than its reaction to *A. amurensis* . In about 20—30% of the cases, there is no reaction, or it is induced only after the ray of the starfish touches the mantle of the mollusk. The assumption that the Yezo scallop is less sensitive to the "scent" of *D. nipon* has been confirmed in electrophysiological experiments on the sensory tentacles of the scallop.

As we have already noted, the reaction of adult Yezo scallops to approaching *D. nipon* and *A. amurensis* under experimental conditions is quite weakly defined. These data are corroborated by observations in a natural environment. There have been many cases where large starfish approached a scallop lying on the bottom, and crawled right over it without even slowing down (Fig. 56).

It has been shown that the strongest escape response of the scallop *Pecten maximus* is observed when it comes into contact with predaceous species of starfish (Thomas, Gruffydd, 1971). Consequently, the weak response of adult Yezo scallops to the indicated species of starfish confirms that the latter are relatively harmless to these mollusks. In the opinion of Thomas and Gruffydd, such behavior on the part of the scallop when harmless species of starfish approach is of an adaptive nature; this type of behavior reduces the energy required by the mollusk to move about and excavate a new hole in the bottom.

Patiria pectinifera apparently poses no danger to an adult scallop. Biryulina's report that these starfish "usually acted jointly, 15—20 of them attacking the mollusk (scallop - V.L.) at the same time" (1972b, p. 49) is probably incorrect; in this case, the divers apparently observed starfish feeding on scallop remains. Cases of underyearling scallops (10—15 mm) being consumed by *Patiria pectinifera* after the mollusks were released onto the bottom have been reported from the scallop plantations in Posyet Bay. However, this was probably a case of starfish feeding on dead mollusks, since the mortality of this size of scallops during stocking is usually quite high. *Patiria pectinifera* does not evoke an escape reaction in the Yezo scallop, even if the starfish are directly on the shell of the mollusk. The experiment has shown that the scallop does not react to *Evasterias retifera* either (Dautov, Karpenko, 1983).

Thus, analysis of the literature and the results of our own observations of natural and cultivated colonies of the Yezo scallop in Peter the Great Gulf have shown that, as a rule, the adult scallop does not play a major part in the diet of starfish. A study of the composition of the food organisms consumed by *A. amurensis* and *D. nipon* in July—August 1981 in Vityaz Bay has shown that 2-year-old scallops are not included in the ration of these species (Bakulin, Levin, 1982). Similar results were obtained in Posyet Bay during the summer of 1982, i.e. only about 1% of the starfish fed on the scallop. It is significant that many of the described cases of starfish feeding on mollusks (Zhyubikas, 1969; Biryulina, 1972b) apply to very large, i.e. old, mollusks. If we take the life span of the Yezo scallop to be 10 years, then 10% of all the scallops should die of old age every year.

At the same time, starfish species such as *A. amurensis* and *D. nipon* can pose some danger to the scallop during the mass swarming of starfish (density of about 0.2 specimens/m^2). The losses of one-year-old scallops at the time of their release onto the sea bottom are especially high. By the end of the first month after their release, the activity of the starfish usually drops to the initial values, but by this time the plantation may have already been badly damaged.

A large scallop (12 cm and larger) can coexist with the largest starfish (up to 3—8 years old) according to our observations.

However, this balance can be upset by a sudden increase in the numbers of starfish, which is sometimes observed. For example, in a local 0.3-hectare area of a large plantation in Posyet Bay, we noted a sudden increase in the abundance of *D. nipon* , which in a relatively short period destroyed 57% of the 4-year-old scallops. At another plantation which was free of starfish at first, a significant number (0.4 specimens/m2) of large *D. nipon* (with rays more than 15 cm in length) appeared in the third year of cultivation; within one year, they essentially destroyed the cultivated scallop population. An increase in the grazing activity of starfish is noted in May—June, September—October, and in the period following a storm.

Consequently, the degree of starfish predation on the scallop depends on a number of circumstances, namely the species of starfish, the size of the animals and the abundance of both species, the composition of the other organisms found in the area, the season, etc.

15.2. Gastropods

According to Belogrudov (1973a), predaceous gastropods of the family Muricidae, primarily *Boreotrophon candelabrum* and *Tritonalia* (=*Ocenebra*) *japonica* , pose a great danger to the scallop in Posyet Bay. Belogrudov studied the consumption of bivalve mollusks by these muricids. In a holding net containing Yezo scallops (15), *Chlamys nipponensis* (1) and *Arca boucardi* (1), which was set out in the sea, *B. candelabrum* destroyed three scallops within the first two weeks. The shells of the eaten mollusks were perforated in 1-3 places. The attack on an adult scallop of the species *T. japonica* was observed in an aquarium. A small cone-shaped craterlet was seen on the upper valve after the first day, the valve (2—2.5 mm thick) was perforated on the fourth day, and the scallop died in three days.

In samples of adult Yezo scallops, traces of boring by gastropods were noted in 27% of the scallops in Minonosok Bay, and in 14% of the scallops in Haloway Bay. At the same time, no traces of boring were found in the sample from Furuhelm Is. (sandy bottom, depth 10—12 m). Consequently, the damage inflicted by muricids depends largely on the habitat of the scallops.

15.3. Cephalopods

Razin (1934) presents some data on the consumption of Yezo scallops by octopuses. He reports that scallop shells with broken off auricles and hinge damage have been found in places inhabited by octopuses (Fig. 57). Zhyubikas (1969) believes that octopuses do not pose much of a danger to scallops, since the former live in very deep waters and prefer a rocky bottom.

In Posyet Bay, the octopus is encountered at most of the scallop plantations and in many of the natural scallop colonies, except for those in shallow sheltered inlets. Octopuses are less common in areas with a flat bottom, where there are no shelters for them or the proper conditions for building them; however, scallop shells of the largest sizes and characteristic breakage have been found here as well. At the entrance to an octopus' lair (under a rock or cliff) in the vicinity of scallop concentrations or nearby, we usually find a barrier constructed of scallop shells. Near this type of shelter at a plantation occupied by a medium-sized octopus (about 0.8 m), this barrier consisted of the valves of more than 60 scallops of the same age (2.5 years old, shell height about 70 mm), i.e. consumed within one incomplete season (observations in August). Due to the scarcity of octopuses, the damage inflicted by them is usually insignificant; however, under some conditions, e.g. when the scallop is kept under *Laminaria* cultivation structures installed on numerous concrete blocks, the number of octopuses can increase, and so does the damage done by them.

15.4. Crustaceans

In natural populations of the Yezo scallop, the young can be eaten up by various species of crabs and hermit crabs during the transition to a benthic mode of life. As the one-year-old scallops settle on the bottom, they become inaccessible to the small species of crabs. Perhaps scallops of this size are part of the diet of the Kamchatka crab which feeds on bivalve mollusks of similar size. This has been indirectly confirmed by the mass migration of crabs from the shores of Posyet Bay after molting. Crushed scallop valves were found everywhere around the plantation on their migration route, which had been stocked with young scallops the day before.

15.5. Fish species

In Posyet Bay, divers observed how young Yezo scallops that fell off the collectors or settled on the bottom were eaten up by flounders. In the opinion of Japanese experts (Kohara et al., 1967), scallop spat are vigorously consumed by flounders and gobies; in fact, during this period, the scallop falls prey more to fish, than to starfish.

16. ABUNDANCE AND BIOMASS

16.1. Population density

Off the coast of Primorye (Maritime Territory of the Soviet Far East - transl.), the colonies of the Yezo scallop occupy an area from 1 to 280 hectares (table 32), but mostly from 2 to 80 hectares (Biryulina, Rodionov, 1972; Bregman, 1979). An even greater area of mollusks has been described in the Sakhalin—Kurile region (Skalkin, 1966). The average density of scallop accumulations in different habitats and in different parts of the same population varies from 0.06 to 1.00 specimens/m^2. The highest density, 7 specimens/m^2, was noted by Razin (1934). According to Ito and coauthors (1975), the optimal density of the scallop during cultivation to marketable size on the bottom is 5 specimens/m^2.

Scallop accumulations can have the form of long, but relatively narrow bands (Preobrazheniye Bay and the Olga Gulf), or occupy wide areas. In colonies, the scallop is distributed nonuniformly. Its dense accumulations (one or several) alternate with areas where its abundance gradually diminishes (Figs. 58, 59). In these zones, the scallop can be encountered either as single uniformly distributed individuals (Melkovodnaya, Preobrazheniye and Zapadnaya bays, off Furuhelm Is., the Olga Gulf), or in small groups distributed in a patchy manner in the same type of area (Haloway and Andreyev bays) (Bregman, 1979).

16.2. Total abundance and biomass

The most detailed research into the distribution and stocks of the Yezo scallop off the coast of Primorye was carried out by Razin (1934) and Biryulina and Rodionov (1972). In addition, Markovskaya (1951) and Bregman (1979) determined the abundance and biomass of the scallop in individual areas along the Primorye coast in 1975. Approximately 40 million scallops inhabited the commercially important 16,000—17,000 hectares off the coast of Primorye in 1932 (Razin, 1934). In the 1940—1960s, the abundance of scallops decreased significantly in the majority of populations, and dropped to nil in some areas. On the whole, the scallop stocks of Peter the Great Gulf decreased approximately 3—fold from 1932 to 1959 (table 38). Over the next ten years, the abundance of the Yezo scallop hardly increased at all, and in 1970 amounted to 5,703,000 for a 906-hectare area of Peter the Great Gulf, with the biomass equal to 1,708,000 kg.

In the areas north of Peter the Great Gulf, new investigations were carried out less frequently, but their results give grounds for assuming that the number of scallops also decreased during the 1940—1970s. For example, by 1975, the abundance of the Yezo scallop in the Olga Gulf had decreased more than 4—fold in comparison with 1932 (table 35).

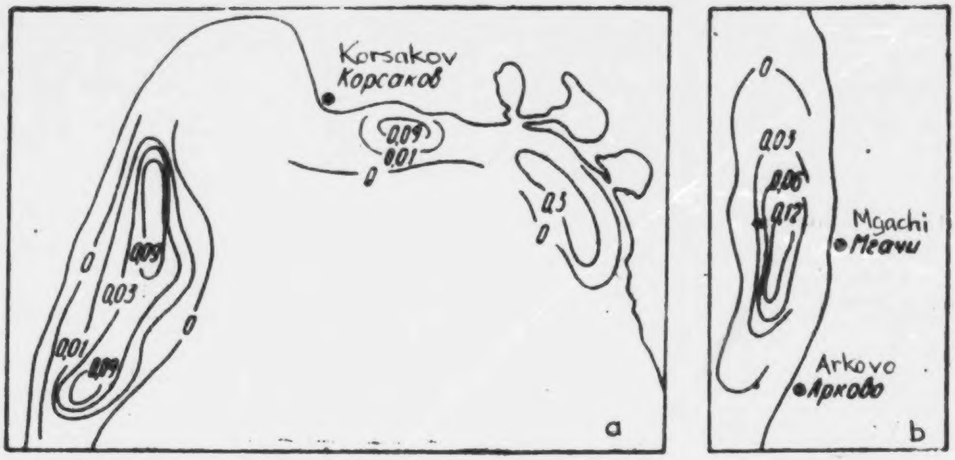
In the opinion of most researchers, the universal decreases in the scallop stocks are due to the intensive commercial utilization of the scallop and the extensive harvesting of it by amateur divers. For example, Skalkin (1971) reports that, by 1969, the biomass of the scallop in the Aniva Gulf had decreased by almost one-half in comparison with 1961—1962, and its biomass in Terpeniye Bay and certain areas of the Kurile chain almost 10-fold (table 34). After commercial utilization of the scallop had been banned off the western shore of the Aniva Gulf in 1966, its abundance increased from 20,000 centners to 24,000 centners in three years.

The abundance of the scallop is greatly influenced by predators, especially starfish. Extensive fouling of the shells by algae (Fig. 8) and parasitization by polychaetes and other sea animals are detrimental to the scallop. The abundance of spat decreases to the greatest extent during the first six months of life, with approximately 96% of the scallops dying off during this period. A high mortality persists throughout the first two years of life (Fig. 60). It then decreases significantly, but as the scallop approaches its maximum age, the mortality rate increases once again.

The mortality of the scallop is irregular throughout the year; it is highest in August (the hottest month of the year) and in winter. This is especially characteristic of the young (Fig. 61).

Table 32. Distribution of the Yezo scalop in different areas along the coast of Primorye (see note at the bottom of p. 35)

Area	Area of concentration, ha	Average density in concentration, spec./m^2	Total abundance, '000 spec.	Average mass, g	Total biomass, centners
Peter the Great Gulf					
Posyet Bay					
Sivuchya Bay	45	0.3	140	280	458
Troitsy Bay	89	0.6	534	179	956
Haloway Bay*	22	0.28	62	—	—
Zapadnaya Bay of Furuhelm Is.	50	0.2	99	—	—
Amur Gulf					
Severnaya inlet of Slavyansky Bay	65	0.9	570	195	1244
Narva Bay	3	2.4	72	346	249
Popov Is. (S)	5	0.5	25	455	114
Reineke Is. (S)	2	0.7	14	369	52
strait between Popov and Reineke islands	17	0.9	153	428	655
Rikord Is.	19	0.3	30	773	210
Pakhtusov Islands	10	0.9	90	708	637
Stenin Is. (SE)	5	0.5	25	684	171
Stenin Is. (S)	10	1.0	100	386	386
Ussuri Bay					
Shkot Is.*	111	0.1	111	—	—
Sukhodol Bay	60	0.2	120	95	114
Andreyev Bay	356	0.7	2492	298	7426
Andreyev Bay*	79	0.32	254	—	—
Cape Zelenyi	10	0.3	30	317	95
Bezymyannaya Bay	30	1.0	300	314	942
From Cape Maidel to Vostok Bay					
Putyatin Is.	18	0.3	54	402	217
Rifovaya inlet	54	0.4	216	405	875
Vostok Bay					
Gaidamak inlet	3	0.3	9	240	21
Srednyaya inlet at Cape Pashinnikov	55	0.6	330	228	752
before Cape Podocenov	36	0.8	288	408	1175
Nakhodka Bay					
Lake Vtoroye	2	0.7	14	258	36
Lake Vtoroye*	279	0.18	501	—	—
Wrangel Bay	18	0.53	36	315	294
Lisiy Is.	1	0.1	1	281	3
North of Cape Povorotnyi					
Melkovodnaya Bay*	15	2.0	300	—	—
Preobrazheniye Bay*	2	4,0	80	—	—
Olga Gulf**	75	—	327	—	—
Olga Gulf*	47	0.16	74	—	—
Vladimir Gulf**	1159	—	6016	—	—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Arkovo
Арково
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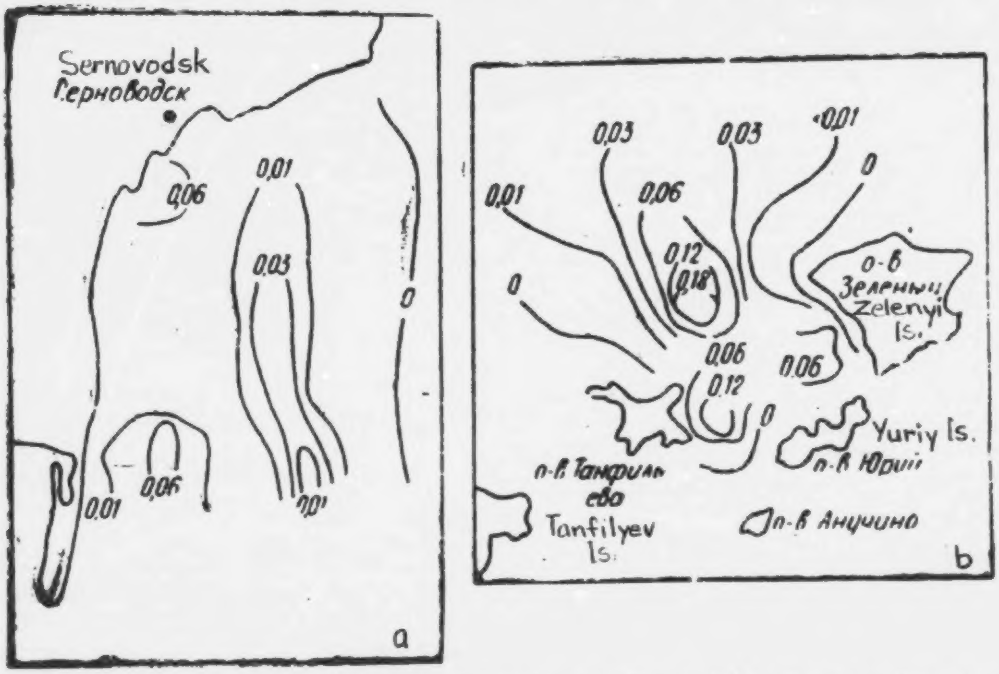
Fig. 58. Density of settlement of the Yezo scallop (specimens/m^2) off Sakhalin Is. and in Aniva Gulf (a) and Aleksandrovsk Bay (b) (after Skalkin, 1966)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Yuriy Is.
о-в Юрий
о-в Танфильева
Tanfilyev Is.
о-в Анучино
b

Fig. 59. Density of settlement of the Yezo scallop (specimens/m^2) off the southeastern coast of Kunashir Is. (a) and the Lesser Kuriles (b) (Skalkin, 1966)

Table 33. Abundance of the Yezo scallop (thousands of specimens)

Gulf or bay	Year 1932	 1959	 1970
Amur	500	349	1079
Ussuri	4710	—	2942
Strelok	3249	2149	—
Vostok	279	53	627

Note: Data for 1932 Razin's (1934), data for 1959 and 1970 Biryulina's and Rodionov's (1972)

Table 34. Distribution of the Yezo scallop in the Sakhalin—Kurile area

Area	Total area of commercial stocks, hectares	Density of settlement, spec./m^2	Biomass, '000 centners		Average mass, g	Total abundance (1969), thou. spec.
			1961	1969		
Aleksandrovsk Bay	2,120	0.08-0.12	—	9	350	2572
Aniva Gulf	107,520	0.03-0.09	43	24	400	6000
Terpeniye Gulf	2,240	Up to 0.04	26	3	500	600
Lesser Kuriles	—	—	—	—	750	—
Kunashir Is.	—	—	100	12	500	1800

Note: Skalkin's data (1966, 1971)

Note to table 32: Table contains Biryulina's and Rodionov's data for 1972; one asterisk marks Bregman's data (1979), and two asterisks Razin's data (1934).

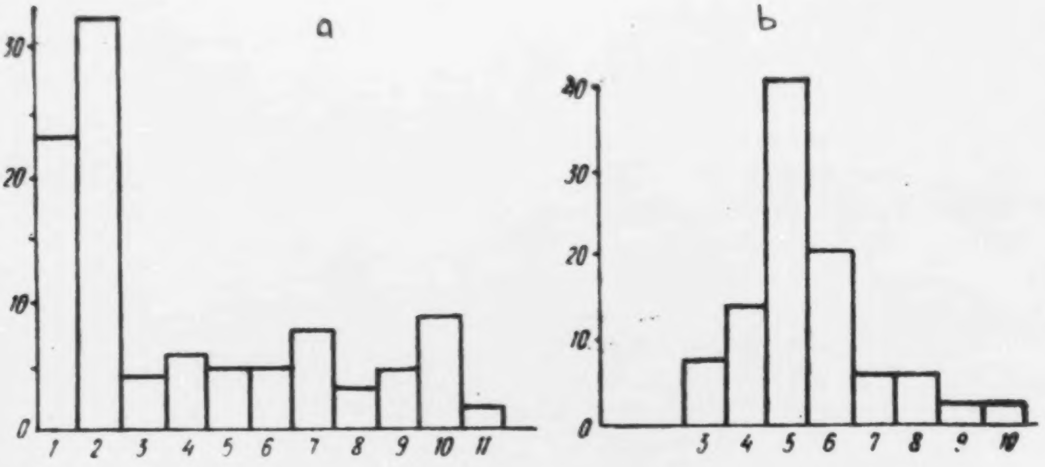


Fig. 60. Age structure of subfossil accumulation (a) and live population (b) of the Yezo scallop in Priboynaya Bay of Popov Is. X-axis - age (years); Y-axis - frequency of occurrence of the Yezo scallop according to age, %

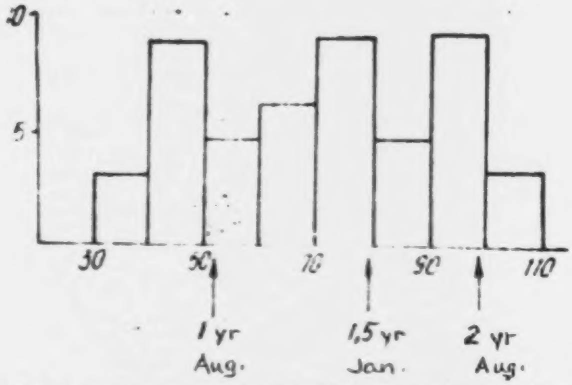


Fig. 61. Fragment of the size structure of subfossil accumulations of the Yezo scallop in Priboynaya Bay of Popov Is. X-axis - height of shell, mm; Y-axis - frequency of occurrence (%) of the Yezo scallop according to shell height. Arrows mark mean values of shell height in August for one- and two-year-old scallops, and in the middle of winter for 1.5-year-old scallops

16.3. Size—weight structure of populations

In the majority of researched populations, sexually immature individuals with a shell height of up to 9 cm are not encountered at all, or are very scarce (tables 35, 36). The largest number of juveniles encountered along with adults was noted in Lake Vtoroye of Nakhodka Bay, where an isolated population occupies a small area (table 32). Spatial separation of the young and the adult animals is highly characteristic of the scallop, and is due mainly to the fact that different age groups prefer different conditions. It may be that the immature scallop strays more than the adult. The latter lives in more crowded conditions because of the necessity to ensure optimal reproduction of the population. The results of a study of the size structure of the same populations during different years point to their great similarity, i.e. to the stability of this characteristic in scallop populations.

Nevertheless, a difference in size composition is observed in populations from different areas of the sea. For instance, 13—16 cm mollusks prevail in the coastal waters of Primorye, and 15—17 cm and larger scallops in the Sakhalin—Kurile area (tables 35, 37).

When we compare the size structure of populations inhabiting various substrates even in closely adjacent areas, we see that the more adverse the substrate, the smaller the scallops. For example, in populations living on a muddy substrate (Haloway and Andreyev bays, Putyatin Is., Lake Vtoroye) or on a predominantly rocky bottom (Lazurnaya Bay), 12—15 cm scallops prevail. On silty sand (Vityaz and Melkovodnaya bays, Olga Gulf, Shkot Is.) and on coarse detrital sand (Priboynaya Bay, Popov Is.), the scallop is slightly larger (14—16 cm). On medium-grained sand in well-aerated regions (Zapadnaya Bay, Stenin Is.), the majority of scallops have a shell height of 16—18 cm (table 35). Consequently, the smallest shells in the same age group are found in the scallops living on a muddy substrate. The same tendency is observed in the well-isolated Busse Lagoon in the Sakhalin—Kurile area, i.e the scallops are smaller on a muddy substrate, and larger on a pebbly one (table 36).

Approximately the same conclusions can be made in relation to the weight structure of a scallop population (table 37); a scallop taken from a muddy substrate is much lighter than a scallop from a sandy substrate. On hard, predominantly rocky substrates (Lazurnaya Bay), they are also heavier than the scallops from a muddy substrate (Andreyev Bay), even if the populations have a similar size composition.

Table 35. Size structure of Yezo scallop populations off the shores of Primorye (Maritime Territory of the Soviet Far East)

			No. of individuals with shell height of (cm):										
Area	Depth, m	Substrate	<9	9-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19
Peter the Great Gulf													
Posyet Bay													
Haloway Bay*	—	Mud	—	12	25	39	24	30	32	17	2	2	—
Vityaz Bay	8	Silted sand	—	—	—	—	1	5	11	15	8	1	—
Zapadnaya Bay	—	Sand	—	6	10	19	10	10	11	24	40	27	6
Stenin Is.	14	Sand	—	—	—	—	—	1	—	4	10	11	5
Ussuri Bay													
Priboynaya Bay of Popov Is.	6	Coarse sand	—	—	—	—	—	10	20	14	3	1	—
Shkot Is.*	7—8	Silted sand	—	—	—	—	1	4	12	13	9	—	—
	7—8	Silted sand	—	—	—	—	4	5	14	10	5	—	—
Lazurnaya Bay*	6	Rocks, sand	—	—	1	2	10	17	8	—	—	—	—
Andreyev Bay*	—	—	—	—	3	4	17	28	71	42	5	—	—
	7	Mud	2	10	3	4	17	22	5	—	—	—	—
Putyatin Is.	8	Mud	—	—	5	3	12	11	10	5	—	—	—
Nakhodka Bay of Lake Vtoroye*	—	Mud	33	3	6	8	31	74	40	19	2	—	—
	3—5	Mud	13	4	14	15	37	55	47	17	1	—	—
Melkovodnaya Bay*	—	—	1	—	8	1	10	31	75	42	13	—	—
	6	Silted sand	2	—	4	8	3	7	18	14	5	—	—
Preobrazheniye Bay	—	—	3	—	1	20	16	41	72	41	6	—	—
Olga Gulf*	—	—	11	1	6	10	13	26	22	18	26	16	—
	10—11	Silted sand	—	—	—	—	—	—	3	19	20	9	—

Note: Table contains our own data for 1979—1981; asterisk marks Bregman's data for 1975 (Bregman, 1979)

Table 36. Structure of Yezo scallop populations based on total mass

Area	Observation date	Condition of gonads	No. of individuals with total mass of (g):								
			0-100	100-200	200-300	300-400	400-500	500-600	600-700	700-800	800-900
Vityaz Bay	12/VI/79	Prespawning	—	—	1	6	14	13	7	—	—
Lake Vtoroye	10/VI/80	Prespawning	17	27	23	68	58	11	2	—	—
Melkovod-naya Bay	10/VI/80	Prespawning	—	5	2	5	14	15	4	3	—
Stenin Is.	19/VI/79	Onset of spawning	—	—	—	1	—	3	7	13	7
Olga Gulf	9/VII/81	Spawning	—	—	—	—	8	22	16	5	—
Lazurnaya Bay	29/VI/80	Postspawning	—	1	5	8	19	5	—	—	—
Andreyev Bay	29/VI/80	Postspawning	6	13	19	23	3	—	—	—	—
Shkot Is.	2/VIII/79	Postspawning	—	—	6	12	9	8	2	1	—

Table 37. Size structure of Yezo scallop populations from the Sakhalin—Kurile area

Area	Percentage of individuals with shell height of (cm):			
	up to 12.0	12.1-15.0	15.1-17.0	over 17.0
Aleksandrovsk Bay	2.1	37.6	57.4	2.9
Terpeniye Bay	—	33.6	68.2	8.2
Aniva Gulf				
western shore	2.8	28.7	57.4	11.1
northern shore	0.4	5.1	45.2	49.3
Busse Lagoon				
SE part, mud*	74.3	25.7	—	—
SW part, pebbles*	18.0	54.0	17.0	1.0
Kunashir Is., SE coast	0.8	16.4	70.4	12.4
Lesser Kuriles	—	4.1	35.8	60.1

Note: Skalkin's data (1966); asterisk marks Kulikova's and Tabunkov's data (1974)

Table 38. Age structure of Yezo scallop populations

Area	No. of individuals of age (years):						
	1-2	3-4	5-6	7-8	9-10	11-12	13-14
Peter the Great Gulf							
Vityaz Bay	—	1	8	14	10	7	1
Stenin Is.	—	1	1	5	11	7	5
Priboynaya Bay	—	10	30	6	1	1	—
Shkot Is.	—	2	16	6	6	6	2
Lazurnaya Bay	—	4	9	2	12	10	2
Andreyev Bay	15	10	14	21	1	—	—
Putyatin Is.	—	22	10	4	4	4	—
Lake Vtoroye	18	34	101	45	7	—	—
Melkovodnaya Bay	2	13	20	11	6	5	1
Olga Gulf	—	—	1	23	16	7	1

16.4. Age structure of populations

The majority of the samples taken from Yezo scallop populations did not contain any sexually immature one- and two-year-old individuals. 11—12-year-old scallops were quite common, and older ones were encountered less frequently (table 38). 5—6-year-olds prevailed in four of the ten samples studied from populations quite distant from each other, and 7—8-year-old scallops prevailed in three of the samples.

The frequency distribution of same-age scallops according to shell height is described by normal curves; their modal values correspond with the mean values of shell size at a full age, while the range reflects the variability of the given characteristic (example given in Fig. 62, A). As we can see, the overlapping of age groups increases with age. Therefore, individuals of the same size may differ in age by a year, or even two.

The recruitment of a population differs every year. For example, there were practically no fourth-year scallops in the 1980 samples from Lake Vtoroye (only 2 of the 208 scallops were fourth-year individuals). In 1969, there were half as many third-year scallops as third- and fourth-year individuals in Troitsy Bay (Fig. 62, B). This type of instability of recruitment is typical of the scallop (Yamamoto, 1950); it is due to the year-to-year differences in the abundance and survival of the larvae.

16.5. Sex ratio in populations

The number of males approximates the number of females in practically all of the populations studied; the occurrence of hermaphrodites does not exceed 0.3—0.4% (Bregman, 1979).

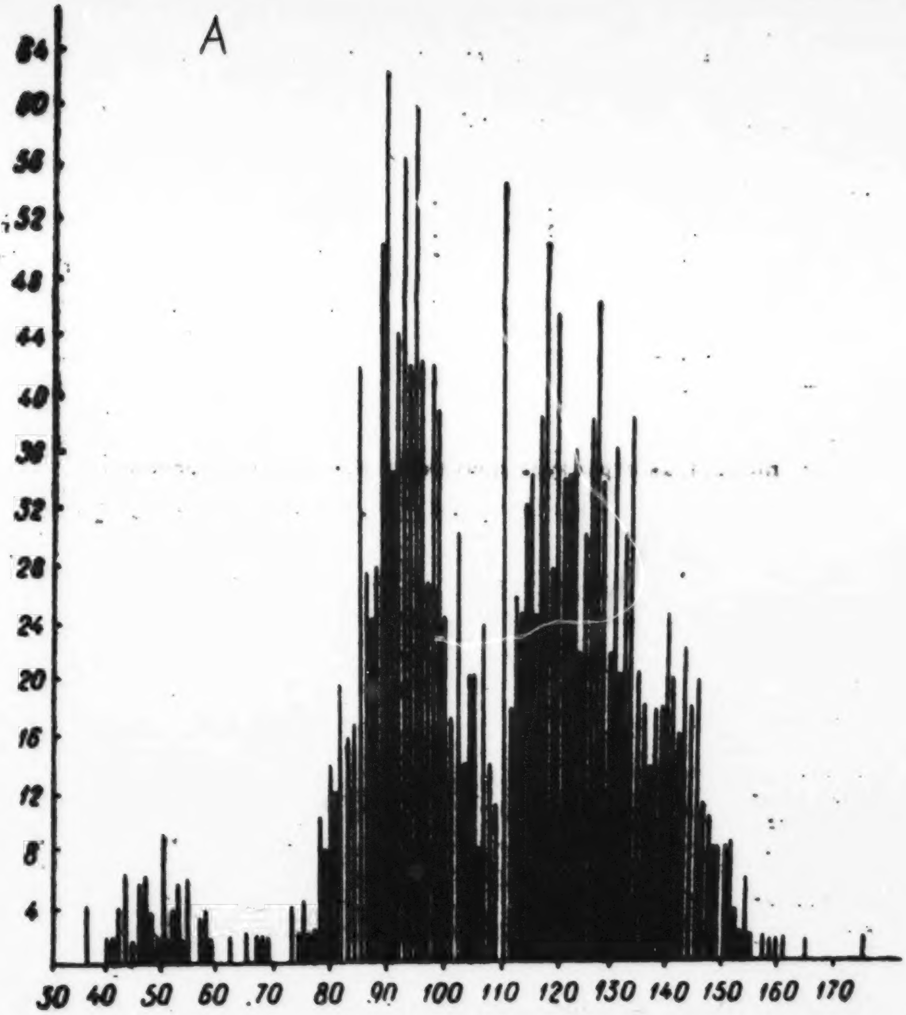
Having compared the male/female ratio in different age groups, we come to the conclusion that males prevail in the younger generations of a population, and females prevail in the older generations. For example, in Lake Vtoroye, there are twice as many males as females (28:14) in the 1—3-year age group, an almost equal number of males and females (46:50) in the 5—6-year age group, and a significantly higher number of females (14:27) in the 7—8-year age group. Approximately the same ratios are observed for the populations of Melkovodnaya and Andreyev bays. About the same tendency is noted in populations composed largely of individuals over five years old. In Vityaz Bay, for example, the male/female ratio is 13:9 in the 5—8-year-olds, and 6:11 in the 9—12-year-olds.

In populations composed mainly of 1—8-year-old scallops, the sex ratio balances out at the age of 5—6 (mostly 5) years, and in "older" populations mostly at the age of 9 years. There are two possible explanations for this, firstly the difference in the mortality rate of the males and females, and secondly the fact that sex changes occur mostly in the males, as evidenced by the presence of hermaphrodites.

Table 39. Production characteristics of some Yezo scallop populations

Area	Observation date, yr	Mean den- of settle- ment, spec/m^2	Mean bio- mass (B), g/m^2	Pg, g/ ($m^2 \cdot yr$)	Ps, spec/ ($m^2 \cdot yr$)	Pg/Ps	P/B	Reference
Posyet Bay	1962-1966	0.1-1.0	128.0	130.0	32.0	4.0	$\frac{P_g}{B}=1$ $\frac{P_s}{B}=0.25$	Golikov, Scarlato, 1970
Minonosok Bay	1972	0.046	4.95	1.18	—	—	0.24	Our data
Haloway Bay	1972	0.039	4.30	1.00	—	—	0.23	Our data
Novgorodskaya Bay	1972	0.015	0.44	0.25	—	—	0.57	Our data
Ekspeditsiya Bay	1971	0.008	0.80	0.205	—	—	0.26	Our data
Zapadnaya Bay of Furuhelm Is.	1971	0.108	12.19	3.20			0.26	Our data
Busse Lagoon	1963-1972	0.200	45.1	14.8	13.3	1.11	$\frac{P_g}{B}=0.32$ $\frac{P_s}{B}=0.29$	Tabunkov, 1974

Note: In our own data, all the values of biomass and production refer to the mass of the soft tissues of the body; the rest of the data refer to the total mass of the body.



(part of Fig. 62)

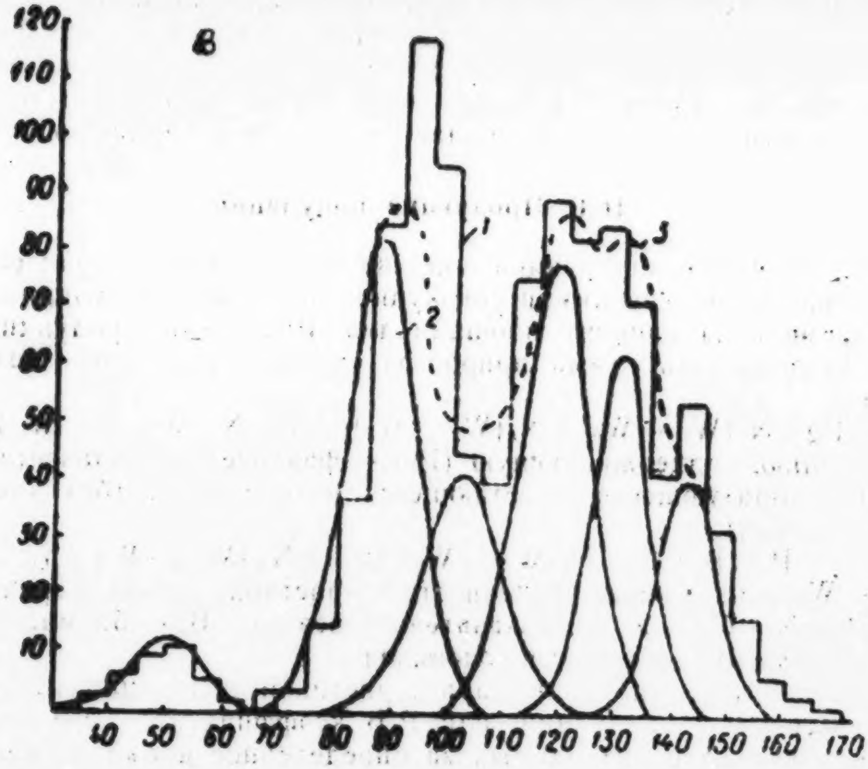


Fig. 62. Size (A) and age (B) structure of Yezo scallop populations in Troitsy Bay of Posyet Bay, Sea of Japan (1969). 1 - actual occurrence of size classes; 2 - theoretical distribution of of size classes within individual age groups; 3 - integral of normal curves. X-axis - number of specimens; Y-axis - shell height, mm

16.6. Production of populations

The term "production of populations" means the quantity of live biomass produced by all the individuals of a population per unit of time per unit of sea floor area. We differentiate between the production of growth (Pg), which is the sum of the increments of mass in each age group, i.e.

$P_g = N_0(W_1—W_0) + N_1(W_2—W_1) + ... + N_n(W_{n+1}—W_n)$, and production of sustenance (P_s), the actual quantity of live matter that is formed and remains in a population (without the eliminated individuals), i.e.

$Ps = B_0 + B_1 + N_2(W_2—W_1) + ... + N_n(W_n—W_{n-1})$, where N_0 and W_0 are the initial numbers of an age group and the average mass of an individual, N_1 and W_1 are the same indices a year later, B_0 is the biomass of the young of a particular year, and B_1 is the biomass of one-year-olds.

An important production characteristic of a population is the value of specific production, or the P/B coefficient, which is the ratio of the weighted average of the products produced over a specific period of time in each age group to the actual average biomass of individuals per unit of area. The value of the production potential (Pg/Ps) also gives us a good idea of the condition of a population. If it is greater than 1, a given population has a fairly good recruitment, and is a stable population. The data regarding these characteristics are given in table 39. As we can see, the P/B coefficients are on the whole quite similar, despite all the differences in abundance, biomass and production. The higher than usual value of this coefficient in certain areas can be attributed to the prevalence of younger age groups, e.g. in Posyet's Novgorodskaya Bay.

17. CULTIVATION

The cultivation of commercially important species is carried out with the purpose of obtaining maximum production, increasing the natural stocks, organizing a regulated industry, and expanding natural reproduction. It greatly reduces the effect of predators, and increases the survival of the cultivated species. According to FAO, the world's aquicultural production increased from 2 million to 6.5 million tons per year over the 1960—1975 period, the percentage of mariculture (cultivation of organisms in the sea) increasing from 20 to 50%, mainly because of the breeding of mollusks such as mussels, oysters, etc. In 1979, it amounted to 9,400,000 tons. The tendency toward increasing the reproduction of mollusks has stayed with us to the present day. Some European countries (Spain, Portugal, France, etc.) harvest from 100,000 to 200,000 tons of mussels and oysters, and so do the USA and Japan.

In the seas of the Atlantic and Pacific oceans, most of the species of the Pectinidae family are utilized commercially. Cultivation experiments have been carried out with only some of them, namely *Argopecten irradians* (in the USA) and *Chlamys nipponensis* and *Pecten albicans* (in Japan). However, the cultivation of these species of mollusks has never been conducted on a large scale.

The Yezo scallop (or the Japanese common scallop - transl.) is a promising maricultural species in the Soviet Far Eastern seas. This is one of the large scallops, which has long been harvested off the shores of Japan and North Korea. In 1966, a ban was placed on its utilization because of the depletion of the scallop stocks in our waters. Since then, intensive research has been conducted to determine the possibilities of cultivating this species.

Japan has had a great deal of experience in cultivating the Yezo scallop. Its intensive utilization of the scallop led to depletion of its stocks, but the measures taken to restore them by collecting the larvae and raising the young have stabilized this process. Today, scallop farming in Japan is developed to such an extent that the output of this branch of industry is comparable to that of the traditional scallop industry, and in some areas even exceeds it. The country as a whole cultivates approximately 30,000 tons of the scallop. The annual spatfall onto collectors amounts to 10—20 billion scallops. Scallop farming in Japan began to undergo intensive development in the 1960s. Apart from Japan, the Yezo scallop is cultivated in North Korea, but there it is raised along with *Laminaria* kelps.

In our country, commercial cultivation of the scallop is carried on only in Primorsky Krai (Maritime Territory of the Soviet Far East), mainly since the 1980s, though experiments began in 1970. The yield since 1983 is about 10—20 tons; the collectors yield up to 30,000,000 juveniles. Experiments on the collection of spat were also conducted in the Busse Lagoon on Sakhalin Is., but they were later abandoned.

Based on the experience of scallop farming in our country, Japan and North Korea, we can single out three essentially possible ways of reproducing this species: 1) all the operations, from the collection of spat to the marketable product, are carried out in a natural environment; 2) spat are obtained as a by-product during the cultivation of algae, after which they are released onto the sea bottom and harvested when they reach marketable size; 3) the hatching of the larvae and spatfall take place under controlled aquarium conditions, after which the young are transplanted to the sea for maturation.

Of these three methods of reproducing the scallop, the first method is the principal one. It is applied both in our country, and abroad. At one time, Japan harvested from 200,000 to one million spat under aquarium conditions, but these efforts did not go beyond the experimental limits, since this method of obtaining marketable scallops is economically unsuitable. The collection of spat from the thalluses of *Laminaria* with subsequent cultivation of them on the sea bottom can be regarded as the most economical method; however, it is apparently used only in North Korea. There is no indication that this method of scallop farming is used in Japan, and spat are very scarce on the *Laminaria* grown in our waters.

The first pilot scallop farm of Primorrybprom (now the "Posyet" Experimental Sea Station) was established in Posyet Bay in 1971. Within the system of Primorrybprom, maricultural units have been established at the "Popov" and "Slavyanka" fisheries, and at the Vladimirsky Agar Plant. The experimental sea station (ESS) in Posyet Bay collects scallop spat onto collectors, and keeps them in holding nets or collectors up to the following spring. In spring, some of the scallops are kept at the station for commercial cultivation, and some are sent to the maricultural units at the "Popov" and "Slavyanka" fisheries, where they are raised to marketable size in holding nets or on the sea bottom. The "Posyet" ESS has the best equipment and the most qualified staff of all the above-mentioned organizations. The entire biotechnology of scallop farming was developed at this station, and is now being tested and put to use there. The system of scallop cultivation accepted at the "Posyet" ESS is described below. It is also described in the manual compiled jointly by TINRO and the Scientific Production Combine of Primorrybolovstvo (Technology..., 1979). The manual is a provisional one, as some of the biotechnological elements will be refined and improved; however, these changes will not be fundamental ones. As mentioned earlier, the highest yield of scallop spat in Posyet Bay was 30 million individuals. In the maricultural unit of the mentioned fisheries, from tens of thousands to hundreds of thousands of spat are obtained on the collectors while the method is being developed.

The cultivation of the scallop is based on the use of the natural ability of the larvae, at a certain stage of development, to attach to a substrate and grow in this attached state for quite a long time. The relative indifference of the larvae to the collector material, as well as the advantages of collectors over a natural substrate (no contact with the bottom, selective placement of collectors, constant monitoring), make it possible to collect large quantities of juveniles within a comparatively limited water area.

The process of cultivation includes the following stages: 1) the collection of the planktonic larvae of the scallop onto collectors; 2) the transfer of older spat from the collectors to holding nets for further growth, or their release onto the sea bottom for commercial cultivation; 3) commercial cultivation in holding nets and on the sea bottom.

When cultivating the scallop, it is necessary to have areas for collecting larvae and for raising the young to marketable sizes. The collecting area should meet the following requirements.

1) It should provide sufficient settling of the larvae (not less than 200 per standard collector);

2) It should be well-sheltered against storms where possible in order to facilitate work on the collectors and holding nets;

3) The water should be clean, and have a temperature of 5—20°C (not higher than 23—25°C) and salinity of 30—33‰ (brief freshening possible to 13‰) during the spring and autumn. The configuration of the bays should create an eddy or slowing of the current, which is conducive to the settling of the larvae onto the collectors. A current velocity of 2—5 m/s is regarded as optimal for the growth of the scallop.

17.1. Settling of larvae on collectors

Observations on the dynamics of abundance of scallop larvae in the plankton enable us to form an opinion regarding the length of the planktonic period in the life of the larvae, their maximum abundance and the periods and intensity of spatfall, and to establish the relationship between the abundance of spat on the collectors and the concentration of larvae in the plankton. Control over the abundance and size of the larvae is necessary for well-timed installation of the collectors.

In Posyet Bay, the larvae grow to 150 μm in about 15 days, and to the stage of spatfall, i.e. to 250—275 μm, in another 7—10 days. Consequently, 22—30 days pass from the onset of spawning up to the time the larvae settle on the collectors.

During the planktonic period, we note several peaks of larval abundance (Fig. 63), due to the difference in spawning time and the influx of larvae from other areas. These factors are also responsible for the significant fluctuations in the size composition of the larvae throughout the pelagic period (Fig. 64). During the first half of this period, the abundance of larvae is usually low. Larvae of different sizes are encountered, but juveniles prevail. The number of settling larvae increases later on, but small larvae are almost always present.

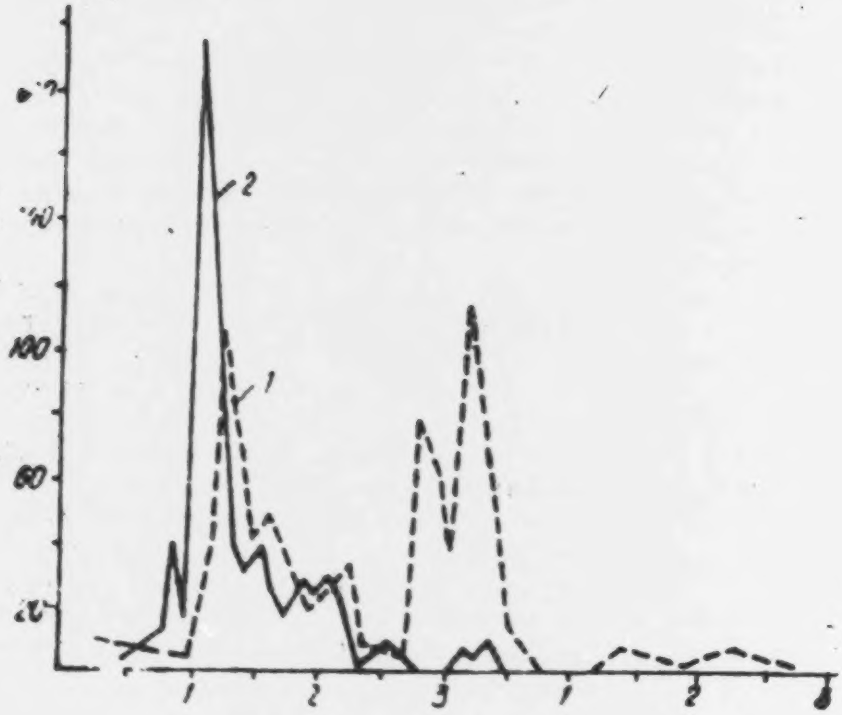


Fig. 63. Dynamics of abundance of scallop larvae in the plankton of Minonosok Bay (of Posyet Bay). 1 - 1976, 2 - 1978. Y-axis - abundance of larvae, specimens/m^3, X - axis - 10-day periods of June and July respectively

After completing the pelagic period of development, the larvae of the scallop attach to various natural substrates with the help of the byssus. The substrates usually consist of certain species of macroalgae and grasses (Golikov, Scarlato, 1970), hydroids, the tubes of polychaetes, as well as pebbles, shell fragments (Yamamoto, 1964) and live scallops (Naidenko, Selin, 1976). In order for the larvae to settle on artificial substrates which are the main element of collectors, they have to be kept in seawater for a certain period of time, during which a thin bacterial—algal film conducive to larval attachment will form.

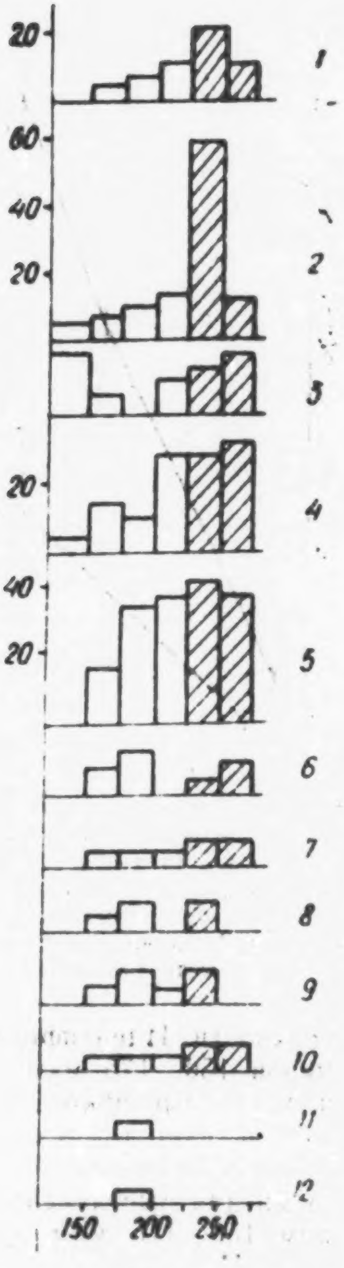


Fig. 64. Size composition of scallop larvae in the plankton of Minonosok Bay (of Posyet Bay) in 1981. X-axis - size of larvae, μm; Y-axis - abundance of larvae, specimens/m^3. Collection dates: 1 - 21/VI, 2 - 22/VI, 3 - 23/VI, 4 - 24/VI, 5 - 26/VI, 6 - 28/VI, 7 - 29/VI, 8 - 30/VI, 9 - 1/VII, 10 - 2/VII, 11 - 4/VII, 12 - 6/VII

The collectors are made of various materials such as caprone, sisal (hemp), the valves of shells. Net collectors consisting of a casing and a filler have been used since 1975. The casing is made of tricot caprone net with a mesh size of 3—5 mm, or of a polyethylene monofilament from which a 70 x 30 cm bag is sewn. A 1.5 m polyethylene net sleeve with a mesh size of 7—12 mm is placed into it. The sleeve is folded in accordion fashion to give the bag a voluminous form. The prepared bags are fastened one after another to form a string of ten collectors.

17.2. Growth of spat on collectors and juveniles in holding nets

One month after the larvae have settled on the collectors, the spat attain a size of about 10 mm; however, individuals varying from 2—3 to 15—20 mm are encountered due to a difference in settling time. The daily average growth over a 60—90-day period amounts to 100—200 µm.

The growth of spat on collectors depends on the time of spatfall, water temperature and the depth at which the collectors are installed. The sooner the larvae settle, the larger the size attained by the same time. For example, in the cold year of 1974, spatfall was late and prolonged; as a result, the spat averaged 5 mm on August 20th. On the other hand, the spat attained a size of 12 mm by the same day during the warm year of 1975, when spatfall commenced earlier (Fig. 65). Similar tendencies were also noted by Japanese researchers (Kohara, Maru, 1970). A size comparison of spat on collectors installed at different depths has shown that the larger mollusks are found on collectors in the upper layers, which is due to the later settling of larvae at greater depths and to better growth in the upper layers (Belogrudov, 1973b; Maltsev, 1976).

For further growth, the spat from collectors are transferred to round or square (cone-shaped or pyramid-shaped) holding nets with a 0.12 m^2 bottom. By the end of the transfer period, the spat attains a size of 20—25 mm. The optimal density for raising scallops from underyearlings to one-year-olds is 20—25 specimens per holding net (Belogrudov, 1981). When cultivating the scallop to marketable size, the density is eventually reduced to 5 specimens per holding net. Depending on their future use, different densities are used in the holding nets. During cultivation in holding nets, the spat are distributed at a rate of 20—25 specimens per holding net (which eliminates the need for another transfer); if the spat are to be later transplanted to the sea bottom or transported to another location, they are kept 200—250 to a holding net till the following spring.

Japanese researchers (Maru, Obara, 1967) note that during winter below-zero temperatures, the growth of underyearlings is inhibited, and yearlings do not grow at all. According to our data, the growth of underyearlings is delayed during the period of below-zero temperatures (Belogrudov, 1981). We know (Tibilova, Bregman, 1975) that scallops of all ages undergo intensive growth at temperatures of 7—16°C from the end of May to July and from September to November; their growth slows down from July to September. Silina (1979) has come up with the diurnal and long-term (7—8 and 13—14-day) growth periods related to the tidal cycles, as well as the optimal temperature range for growth (10—14°C).

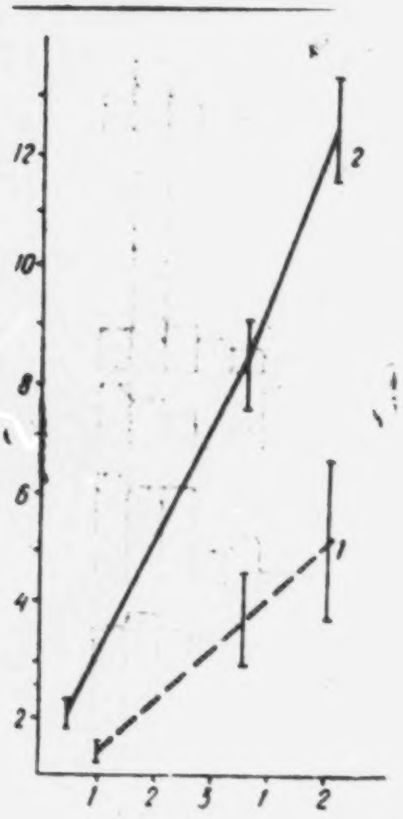


Fig. 65. Size of scallop spat on collectors in Minonosok Bay in 1974 (1) and 1975 (2). X-axis - 10-day periods of July and August respectively; Y-axis - size of spat, mm (based on shell height)

The highest growth rates of the scallop are observed up to the fourth year; a decrease in growth rate is noted during the fourth year (Yamamoto, 1964; Maru, Obara, 1967; Silina, 1979). It has been established (Belogrudov, 1981) that the scallop grows better in open-sea areas, than in coastal ones, which is due to more stable hydrochemical conditions (the absence of runoff and freshening) and favourable temperatures (the absence of summer warm-up and winter supercooling).

17.3. Collection and rearing of spat

In Posyet Bay, the scallop begins to spawn in the middle—end of May, and completes the spawning period in the middle—end of June. In other areas of the Far East, spawning takes place 1—1.5 months later. In areas where the scallop is cultivated, it is necessary to keep track of the temperature at the bottom, at the surface and at the 5-metre level all year round; this makes it possible to better predict the quality of spawning and the fluctuations in the abundance of scallop larvae in the plankton and the abundance of spat on the collectors.

Once every 10 days from May to June, gonadal maturity is determined visually and on the basis of the gonadal index in 25 scallops from different bays. These samples are taken once a week from the onset of spawning and up to its completion. Ten days after the onset of spawning, plankton samples are taken daily with an Apstein net in the bay where the spat are to be collected. Plankton surveys are conducted (2—3 times daily) to study the horizontal distribution. The stations should be uniformly distributed over the water area of the bay, at a distance of about 100—200 m from each other. Total removal from the bottom to the surface is carried out at each point. Identification of the larvae is reliable when the latter attain a shell height of 150—175 μm. By regular examination of the plankton samples, we can trace the growth of the larvae and the increase in their numbers, as well as the distribution in a given water area. The best sites for collectors will be those where the concentration of larvae is constantly high. When 150—175 μm larvae are detected, collectors should be set out within a 7—10-day period. With an abundance of scallop larvae in the neighbourhood of 100 specimens/m^3, at least 400 specimens should settle on one collector. This gives us an idea of the optimal number of collectors.

According to TINRO recommendations, the collectors are placed on a set-up consisting of a 100 x100 m frame made of 50-60 mm caprone ropes fastened at the corners with anchored stays. Inside the frame, working ropes (mainlines) are strung at 5 m intervals. The whole set-up is kept on the surface by spherical glass floats spaced 1 m apart. The "Daltekhrybprom" Research and Production Association has developed different types of these set-ups and their technical specifications. Strings of ten collectors on vertical ropes (leader ropes) are suspended to the working ropes of the set-up at one-metre intervals. A weight of about 0.6 kg is tied to the end of each string of collectors. Depending on the depth, the collectors are placed 6—10 metres from the surface of the water so that they do not touch the bottom. One of these set-ups holds a total of 2000 strings of collectors.

About 10—15 days before the scallops are transferred, we determine the total number of spat; from the 1st, 10th and 20th mainlines at the beginning, in the middle and at the end, three collectors (upper, middle and lower) are taken from a string, and a visual count is carried out. The average density of spat in a collector is multiplied by its total quantity. The collection of spat from the collectors begins when 80% of the spat has attained a 10—15 mm size. If there are no starfish or other enemies of the scallop in the vicinity, it is best to transfer the scallop at the latest possible time.

The holding nets into which the spat are placed are made of netting with a 5 mm mesh size; each holding net has an opening that is closed with a draw string. The collectors are disassembled on a specially equipped pontoon. The spat are placed in a flow-through holding net on the pontoon. After thorough sorting and removal of mussels, starfish and other animals, the spat are distributed 200—250 per holding net. The holding nets are then tied one metre apart in strings of ten, and suspended at the 5—8-metre level. This set-up is submerged several metres for the winter as protection against storms and ice.

In the case where the spat are to be shipped to other places for cultivation, they are removed from the collectors in autumn, when they have attained a size of 20 mm on the average; they are transported by "MPC-225" vessels. Household galvanized tubs with a holding capacity of 60 litres or wooden cages with 7—10 mm holes in the bottom are used as containers. The latter are filled 1/2 or 2/3 with spat, and covered with canvas for protection against the sun and wind. Enroute, the scallops are sprayed with seawater from the ship's fire pump for 2-3 minutes every 30 minutes. Containers specially built for transporting spat and one-year-old scallops have been successfully tested at the Far Eastern branch of the "Promrybolovstvo" Research and Production Association and the Primorye Production Acclimatization Station.

17.4. Commercial cultivation, harvesting and shipping

The suspended and bottom methods are used for commercial cultivation of the scallop. By the suspended method, the scallop is raised in holding nets suspended in the water. As the scallop grows in the holding nets, they are transplanted several times to reduce the density per holding net. Transplantation is carried out in April, after the set-ups submerged for the winter have been raised. The density of stocking should be about 25 specimens per holding net during the first year of cultivation, 10 specimens per net in the second year, and 5—7 specimens per net during the third year (table 40).

Table 40. Sequence of transplantation of scallops at the "Posyet" Experimental Maricultural Station

Year spat collected	Age	Time of transplantation	Density of stocking, spec./net	
			I	II
1979	2-3 mos.	Sept—Oct	200	20
1980	0 +	April	25	20
1980	1 +	August	25	20
1981	1 +	April	10	10
1982	2 +	April	5—7	10
1983	3 +	April—May	Harvested	Harvested

Transplantation operations are carried out on a pontoon or on shore. The strings of holding nets are hauled in, the opening untied, and the scallops dumped into tubs containing water or into the holding tank of the working pontoon. In the process, extraneous animals and empty shells are removed. The required number of scallops is placed into a holding net through its opening, and the string is drawn. Then, strung together, the holding nets with the scallops, are set out for further cultivation of the scallop. The scallops must not be allowed to dry out, or be exposed to direct sunlight or rain for long periods.

In October, the strings of holding nets are lifted onto the pontoon, and the fouling removed from them with a brush and water. In the case of extensive fouling, the mollusks are transferred into clean holding nets. After defouling, the set-up is submerged so that the holding nets are 1.5—2 m from the bottom, after which a diver checks the installation of it to see that none of the nets are touching the bottom.

Cultivation of the scallop on bottom plantations requires sandy-silty or silty-sandy substrates with an admixture of shells, gravel and pebbles, and with a minimal number of starfish. The content of finely divided silt (particle fractions 130 µm) should not exceed 30%. The depths of the plantations should not be less than 3 m in sheltered bays and not less than 10 m off the open coastline to prevent the scallop from being cast out on shore during storms. Preference is given to those areas where the scallop is concentrated today, or was in the past. If starfish are abundant at the transplantation site, dredges or traps baited with fish remains, etc. are used to catch them. Bearings are taken of the selected part of the bottom from a vessel using shore reference points. The setting up of buoys at the corners of the site, or one buoy in the centre, is a more reliable method of mapping.

During bottom cultivation of the scallop, the latter is scattered from the stern of a vessel at a rate of 8—12 specimens/m^2 of the bottom during the drifting or low-speed travel of the vessel. The work after that consists of controlling the numbers of predators (starfish, gastropods). The cultivation period is 3.5—4 years.

At the final stage of suspended cultivation, all of the scallops are taken from the holding nets, even those that have not attained marketable size. When harvesting scallops from bottom plantations, individuals with a shell height of less than 10 cm are not taken.

The harvesting of scallops on bottom plantations is carried out by divers. When a suitable dredge or trawl is developed, the mollusks should be harvested by mechanical devices. The scallop is harvested in a given area once in 3—4 years; therefore, the young should be alternately spread to different areas over the 3—4-year period. The harvested scallops are shipped to the receiving point for processing from the end of March up to the middle of May, and in September—November.

17.5. Benthic period of life

The transition to a benthic mode of life in the scallop begins upon the completion of metamorphosis, from the moment the fully formed juveniles detach themselves from the substrate. In southern Primorye, this usually occurs in autumn. The detached scallops measure 1.3—2.5 cm (Maru, Obara, 1967; Belogrudov, 1973b). The beginning of the benthic period is a critical time for the scallop, for it is during the first months of life on the bottom that the highest mortality is observed, and only a small number of individuals survives in a natural environment (Yamamoto, 1964; Golikov, Scarlato, 1970; Naidenko, Selin, 1976)., and the smaller the juveniles, the higher the mortality. When the scallop is cultivated, this moment is somewhat less critical because juveniles with a shell height of more than 30 mm that have been raised in nets or on collectors settle on the bottom (Yamamoto, 1964; Kan-no, 1970;

Sanders, 1973; Technology..., 1979; Gelogrudov, 1981). In this case, the survival of the scallop increases significantly to tens of percent (Kalashnikov, 1981).

Only two of the papers known to us describe the behavior of a young scallop on the bottom. Volkov and coauthors (1982) planted 500,000 one-year-old scallops in several study areas in Vityaz Bay with a density of about 1000 specimens/m^2. In these study areas, the scallop migrated over a distance of tens of metres, in some cases going in the opposite direction. Starfish moved parallel to the scallops, the highest densities of scallop and starfish distribution coinciding. Morgan and coauthors (1980) released 25—45 mm scallops of the species *Argopecten irradians* at an initial rate of about 90 specimens/m^2. Over a period of 10 days of observation (10 appears to have been corrected to 70 by hand - transl.), the density on one of the sides of the study area (15 x 15 m) decreased to 10—11 individuals/m^2, and then in the 9 weeks of the experiment to individual scallops per square metre. At the same time, the whole mass of scallops moved several metres shoreward, occupying a large area. The authors attribute the migration of the scallops to the effect of tidal currents, which was also noted by other researchers (Moore, Marshall, 1967).

We located our study areas stocked with young scallops in a sheltered bay protected from wave action and strong tidal currents. When planted on the bottom, the mollusks moved about "restlessly", the intensity of their movements peaking within the first hours of their release; the movements themselves were of a random nature. The higher the initial number of scallops in a study area (0.5 x 0.5 m), the higher the rate of decrease in the density of settlement. An intensive drop in the number of animals occured within the first 24 hours or slightly more. After that, the migrations of the scallop became less frequent, and the density of its settlement in the study area showed a tendency towards stabilization. Experiments with different densities have shown that the final concentration of the scallop is directly proportional to its initial density. The adaptability of the animals also plays a part. During the period of adaptation on the bottom, the scallop rarely travelled farther than two metres from the centre of a given study area. Most of the mollusks stayed within these boundaries, and only individual specimens later migrated up to 4 m.

Adult scallops (shell height 10—12 cm) were released under the ice at a rate of 60 specimens/m^2; a holding net was used to keep them in the study area for the first few days. Under these conditions, 1/3—2/3 of the mollusks buried themselves firmly in the bottom substrate (Fig. 66), while the rest remained on its surface and continued to move about. When the holding net was removed, all of the active individuals went beyond the boundaries of the study area, occupied a one-metre strip along its periphery, and buried themselves in the ground. From time to time, some of the scallops moved to another place within the given zone, but their migrations were apparently induced by the presence of the diver conducting the study.

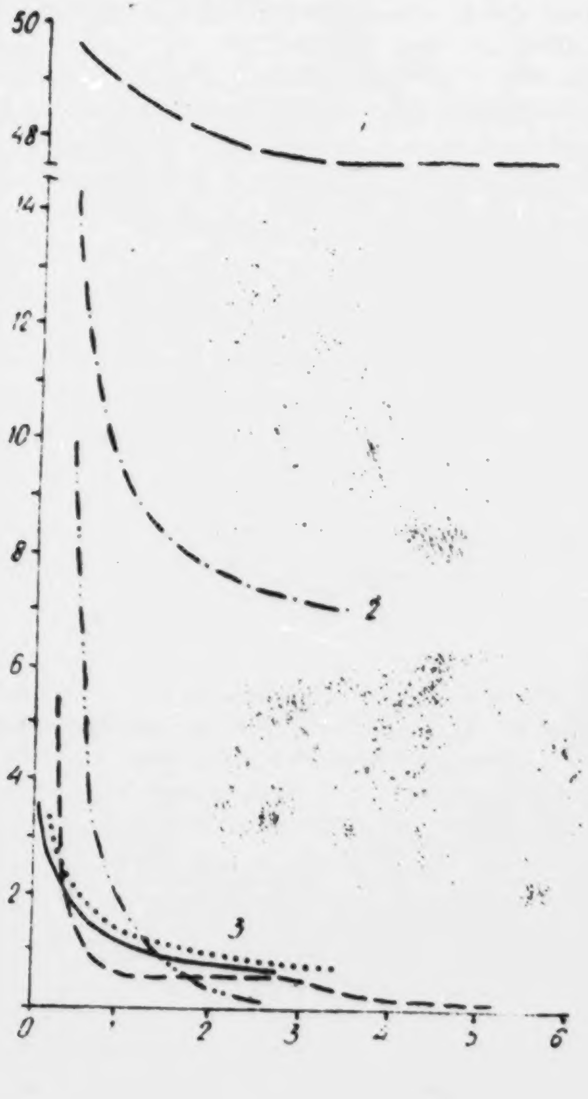


Fig. 67. Dynamics of scallop density on bottom plantations. 1 - plantation in a sheltered bay, 2 - plantation in a partly sheltered bay, 3 - plantation in an open water area. X-axis - time, yr; Y-axis - density of scallops, specimens/m^2

What caused the dispersal of the scallops on the bottom? It is assumed that each individual strives to acquire its "own territory" (Akira, 1980). On the other hand, when the density decreases, the mollusks do not strive to move away from each other; in fact, they gather in groups of several individuals. On plantations with a high content of silty fractions in the substrate, the scallops change places more frequently. On parts of the bottom with a lower sedimentation rate and sandy substrates, adult mollusks rarely change places. The accumulation of silt on the upper valve of the scallop shell may be the cause of the frequent changes on a silty substrate.

The higher the density gradient, the more intensive the dispersal of the scallops. In the case of initial "saturation" of the area being stocked (e.g. in a sheltered bay) or the stocking of a vast water area measuring tens of thousands of square metres, the dispersal of the scallops is inconspicuous, and is observed only on the edge of the plantation. Kan-no (1970) describes the stocking of an area of bottom with 500,000 juvenile scallops at a rate of 1.34 specimens/m^2. After 18 months, 88.1% of the animals had survived.

The assumption that the scallop can direct its movements to escape starfish (Volkov et al., 1982) seems improbable. During observations in the study areas, the scallops that found themselves close to a starfish retreated, but other scallops immediately turned up on the path cleared by the predator. Though a decrease in the density of scallop settlement occurred in this case, it was caused mainly by the fact that some of the animals left the study area.

With the use of the tagging method, it was found that two species of scallops, *Amussium japonicum* (Williams, Dredge, 1981) and *Placopecten magellanicus* (Posgey, 1981) are capable of migrations. Tagged mollusks were released into the sea, and then 1—2.5 years later, their positions were recorded from the commercial take of scallops. The information obtained in both studies shows that the migrations of these scallops did not exceed 2 km (less commonly up to 10 km). These authors conclude that the scallop does not perform lengthy migrations, and the observed displacements coincide with the axis of a strong tidal current.

On commercial plantations in Posyet Bay, the decrease in densities in the open parts of the bay during 1973—1979 varied from 3.5—9.6 to 0.5—0.8 specimens/m^2 from the very first year after stocking. In the sheltered inlets of the bay, the decrease in density is inconspicuous, even with an initial density of up to 50 specimens/m^2 (Fig. 67). After the "Elis" typhoon in 1982, all of the unsheltered plantations at depths of less than 20 m were destroyed.

The quantity of scallops cast out on shore in the study sector constituted at least 16% of all the scallops counted on the bottom. The main commercial accumulations and plantations of scallops are located in the shallows (up to 20 m) of Posyet Bay. Wind-blown and surge waves that follow typhoons are particularly dangerous here. Mass mortality of benthic invertebrates, including the scallop, are also brought on by freshening and by high waters followed by intensification of currents (Egglleston, Hickman, 1972; Andrews, 1973).

Therefore, the scallop apparently does not migrate extensively, despite its ability to move freely along the bottom (Baird, 1958; Hartnoll, 1967; Moore, Trueman, 1971; Dautov, Karpenko, 1983). The migrations of this mollusk are irregular and undirected; they can be increased as a result of hydrodynamic factors, but these movements are by no means migrations.

18. HARVESTING AND PROCESSING

The history of man's utilization of mollusks dates back to ancient times. Shells have long been discovered during archaeological diggings not only in coastal regions, but also in areas thousands of kilometres away from the sea.

All of the shells found during excavations can be classified into two groups. Some of them brought man aesthetic pleasure, while others contained his food. Excavations of the palace of Minos, the ruler of Crete, uncovered a vast quantity of shells, among which experts identified more than 9 genera of edible gastropods and bivalve mollusks. Accumulations of shells similar to those discovered on Crete and known as "kitchen midden" have been found along the shores of Denmark, Sweden, Bretagne, Portugal, North Africa, South Asia, in the cultured beds of the Stone Age of Japan and northwestern America. Not only along coastlines in almost all of the ancient settlements along the Central Dnieper, in Kiev and the Tripolye do we encounter vast accumulations of bivalve shells which also form a type of "kitchen midden" up to 0.5 m in thickness. Pits filled with shells to a depth of even more than 1 m have been found in Kiev (Burukovsky, 1977).

Palaeontological and archaeological research data indicate that the population of the coastal areas of the Far East have long been closely associated economically with marine organisms which primarily served as a source of food (Krasnov et al., 1977). Mollusks were by far not the last on this list. Beginning with the Palaeolithic Period (25,000—30,000 B.C.), the coastal inhabitants of Peter the

Great Gulf gathered edible mollusks. At the end of the second—beginning of the first millenium B.C., a distinctive culture of shell mounds called the "Yankovskaya" culture spread throughout many areas of the Far East (Okladnikov, Derevyanko, 1973). The most abundant accumulations of sea shells in Primorye were discovered on the shores of the Amur and Ussuri gulfs. A study of the composition of these shell mounds has shown that *Rapana* , mussels, oysters and scallops were the favourite food of the coastal inhabitants of Sakhalin Is., the Kuriles, Primorye, Korean peninsula and the Japanese islands. The shells of 5 species of gastropods and 15 species of marine bivalves have been found in the ancient settlements of man in the Far East (Krasnov et al., 1977).

In the Stone Age, mollusks were an important part of the human diet, for the nomadic hunters turned to a settled way of life. Settlement on the seacoast, river bank or lakeshore provided man with this easily accessible food.

The Maya Indians, one of the most advanced civilizations of Central America, used shells for decorating public buildings, as a symbol of reverence for the dead during burials, and as vessels for storing nephrite and cinnabar, valuable religious symbols (Cox, 1979).

Shells became a cult object. Shells were known and revered in the land of Sumer, one of the greatest civilizations of antiquity. Precious minerals and metals were fashioned into jewellery, cups and candlesticks shaped like shells. Shells were used for pictures and frescoes. Stylized shell images were widely used for decorating palaces (Burukovsky, 1977).

During excavations in Anatolia and Greece, statuettes of Aphrodite emerging from the scallop shell were found quite often; the shell was often seen on the garden walls of Pompeii, in the mosaics of Herculaneum, in the niches of ancient temples. The scallop was particularly common on burial monuments. It adorned the lead coffins of Rome's Bretagne and the marble sarcophaguses of Asia Minor, as well as Byzantine tombs.

In the 11th century, the scallop *Pecten jacobeus* became the symbol of Palestine pilgrims to "Christ's grave", who attached the lower, more convex valves to their clothing. In the 15th century, the knight crusaders decorated their armour with scallop valves. The latter were later used in the coats of arms of some high-born families, descendants of those who took part in the crusades.

At the end of the 17th century, classicism in art was replaced by refined rococo. The name of this style originated from the French word "rocaille" which in translation means "a shell ornament". Shell ornaments formed the basis of this style which reached its acme during the first third of the 18th century. In the 19th century, the British—Dutch oil company "Shell" made the scallop shell of Saint Jacob its emblem.

18.1. Harvesting of scallops

Species of the family Pectinidae are found in practically all the seas and oceans. During the 1960—1970s, the scallop placed third in the yield of bivalve mollusks (7.6%, or 114,000 tons, in 1963). In 1963, the yield of scallops amounted to 86,000 tons in the USA, 9000 tons in Japan, 7400 tons in Canada, 7100 tons in France, 2900 tons in Australia, 900 tons in England, 200 tons in Spain, 100 tons in Iceland, and 400 tons in all the other countries (Martinsen, 1966).

In 1938, the world's take of scallops amounted to 61,000 tons. Gradually increasing, it reached its maximum (180,000 tons) in 1966, after which it began to decrease gradually, dropping to 140,000 tons in 1970 (Martinsen, 1972).

According to the data available to us, the following pectinids belong to the marketable species: *Pecten maximus* , *Mizuhopecten yessoensis* , *Placopecten magellanicus* , *Argopecten irradians* , *Argopecten gibbus* , *Swiftopecten swifti* , *Chlamys patagonica* , *Chlamys albidus* and *Chlamys opercularis* .

This list is far from complete, since many of the research papers do not indicate the species name of the scallop.

Accumulations of commercial pectinids are known off the coast of the British Isles (Mason, 1978, 1983), Australia (Heald, 1977), Japan (Martinsen, 1960; Martinsen, Sadykhova, 1966; Wakui, 1979), the USSR (Razin, 1934; Skalkin, 1966; Myasnikov, 1982), and both Americas (Posgay, 1968; Broom, 1976; Lasta, Zampatti, 1981). Fishing for *Placopecten magellancicus* off the northern coast of America has been going on since 1880. During the initial years, the yield amounted to 100 tons of meat per year. The record catch (17,000 tons) was made in 1962. In the 1970s, the take dropped to 8000 tons a year (Posgay, 1979). On the western coast of Australia (near Abrolhos Is.), the scallop industry took off in 1967, when 23.1 tons of mollusks was caught (live weight with the shell). The following year yielded 129.3 tons; in the years that followed, the scallop trade was not conducted on a regular basis. It was renewed in 1980, and a record catch of 1050 tons (or 210 tons of meat) was made in 1984 (Record catch..., 1984).

From 1946 to 1961, Japan's scallop industry was conducted mainly in the vicinity of Hokkaido. The average annual catch on the side of the Sea of Okhotsk amounted to more than 70% of the total Hokkaido yield, i.e. 965 tons (Martinsen, Sadykhova, 1966)

Up to the 1920s, the scallop industry on the territory of Primorye (Maritime Territory of the Soviet Far East) was uncontrolled. The very first data concerning it appeared in 1920, when the scallop catches in Primorye reached 1200 tons. The industry almost ceased to exist after that (Skarlato, 1981).

In 1929, Dal'gosrybtrest (Far Eastern State Fishery Combine) in Peter the Great Gulf (Wrangel Bay) set up an experimental scallop enterprise. The scallops were caught with a trawl from a motor kungas [(Far East) an open fishing vessel with a capacity of 3-5 tons]. No large accumulations were detected. The yield amounted to about 50,000 scallops, or 167 kg dried weight. In 1930, the same Combine was the first to organize a widescale scallop industry in northern Primorye and Peter the Great Gulf, where the operation included six kungases with divers and small boats with one catcher. In three months of fishing, 160,000 scallops were caught in Razboinik Bay, about 29,000 scallops in Preobrazheniye Bay, and 178,000 in Vladimir Gulf.

Prior to the 1930s, no scientific research was conducted to study and assess the stocks of commercial mollusks in Primorye. In 1931—1932, TINRO together with other scientific institutes began to conduct extensive research in all of the Far Eastern seas. Under the supervision of A.I. Razin, an expedition was launched to establish the stocks of commercial mollusks in the Sea of Japan, from the Korean border to the Vladimir Gulf, and then in the Strelok, Amerika and Ussuri bays.

From 1933 to 1937, after TEMP (literally Trust for the Exploitation of Marine Products) had been organized in Vladivostok, the yield of scallops amounted to about 900 tons a year (Martinsen, Sadykhova, 1966).

In the 1960s, the scallop industry was started up again in the waters of Primorye. Divers harvested the scallops in Peter the Great Gulf, while dredges and trawls were used from small seiner-type vessels in the Sakhalin-Kurile area. It was soon found that the natural stocks of this mollusks were insufficient to meet the growing demand for sea produce.

For more than a decade, research has shown that the large stocks of scallop are confined to specific areas. The scallop is encountered even today in the places once described by Razin as being abundant (Razin, 1934).

Off the shores of Sakhalin Is., in Aniva Gulf, the commercial use of the scallop was begun by Sakhalinrybprom in 1961. In 1962, the catch for all the areas (Southern Kuriles, Aniva Gulf, Terpeniye Gulf) amounted to 5300 tons, and in 1963, it totalled 2300 tons. In Terpeniye Gulf, the scallop was harvested only one season, and never again since 1962 (Skalkin, 1966).

18.2. Fishing gear and fleet

Gathering was one of the main types of activity of primitive man. The latter could have gathered mollusks when they were cast out on shore during storms, or when they were left on sand-banks during low tide, or if they inhabited shallow lagoons or rocks projecting from the water, where they could be easily gathered. Later, man began to invent different devices for harvesting edible mollusks.

Up to the beginning of the 19th century, the local population of Primorye used the most primitive method to catch edible mollusks, namely wooden dredges with metal teeth. The mollusk was also caught with a rope pulled along the bottom, which the mollusk grasped if it happened to get between its valves. It was also caught from boats with the help of a "mirror" (a box in which one side was replaced by glass though which the animals could be seen) and a scoop net (Razin, 1934).

Even with the use of these technical devices, not more than 400 scallops were caught in one day. In Primorye, the use of divers for marine invertebrates began in 1919. The yield of scallops increased significantly, one diver harvesting up to 9000—12,000 scallops daily (Bazikalova, 1930).

The simplest to make and the most productive was the toothed dredge which resembled a large rake with a 2-panel bag attached to it (upper panel consisting of thick trawl netting, lower panel of a ring net). The size of the dredge depended on the type of vessel used.

For small seiner-type vessels, a dredge with a frame up to 2.5—3 m wide and 30-35 cm high (length of teeth) is used. The distance between two adjacent teeth should not be less than 12 cm. According to the observations of divers in the Aniva Gulf in 1962, in areas with large quantities of algae, seaweed, coarse fragmental material and large slow-moving animals (starfish, etc.), dredges with teeth this far apart collect large mounds ahead of them, which push the scallops aside or pass over them. Therefore, dredges with sparser teeth should be used to harvest scallops.

The length of the dredge bag varies from 2 to 3 m. The ring net consists of a set of rings 40—60 mm in diameter and 5—6 mm in thickness, which are connected by a steel wire 6 mm in diameter. A net made of a steel-wire rope is often used instead of a ring net. Along the lower edge of the bag's neck in the metal net, there is a small net which is attached with a slight dip to the teeth of the dredge; instead of a chain, a set of thin metal panels (which increase the productivity of the dredge) can be used. The bag of the dredge ends in a brace shank consisting of an iron tube or a strong wooden pole 40—60 mm in diameter, and has a zipper slightly higher.

Trawl heads consisting of two brackets interconnected anteriorly by a cross-piece are attached to the frame of the dredge. A spacer is sometimes centered between the cross-piece and the frame of the dredge. The trawl heads are up to 1 m in length and 20 cm in height. Sliding brackets which are not fixed on the frame and do not have a cross-piece and spacer are also used.

The frame and teeth of the dredge are made of steel and rod iron up to 30 mm in diameter, and the trawl heads of iron 20 mm in diameter. Some joints of the dredge are riveted or welded (Skalkin, 1966).

True, in the *Chlamys albidus* stocks off the Northern Kuriles, we managed, with a dredge shaped like an equilateral triangle with the long side measuring 1.5 m, to obtain the same catches as with a toothed dredge at the same site. This dredge is made of wire 30 mm in diameter; the bag is made of trawl netting with a mesh size of 20 or 50 mm, depending on the trawl target, and three 1.5—2-metre leader ropes are attached to the corners of the dredge.

At the end of the 19th century, the scallops off the Japanese islands (mainly around Hokkaido) were caught with dredges from boats, and later from motor vessels.

The following types of fishing gear are used to catch scallops of the genera *Chlamys* and *Argopecten* in the Atlantic Ocean (Broom, 1976). On flat sandy bottoms, the scallop was caught with light triangular dredges with a toothed or lobed rake (for embedding the dredge into the bottom). A dredge 8 feet long (2.44 m) and weighing 178 kg, which moves along the bottom on 2-3 rollers placed at the mouth of the bag, was used for work on rocky bottoms. A chain groundrope is used instead of a lobed or toothed rake. The bottom of the bag is made of steel rings, and the top is made of sisal or courlene netting. In another type of dredge, the rollers are replaced with bobbins; this type is considered to be more effective on hard bottoms, for bobbins often get stuck in soft substrates. Since the scallop is a good swimmer, beamtrawls and otter trawls, which are higher than dredges, must often be used. Two—three chains are used to scare the scallops to the surface. The usual beamtrawl is 8 feet (2.44 m) wide, and has a tubular steel beam 18 inches (45.7 cm) above the sea bottom. The bag is made of courlene netting with a mesh size of 60 mm, while the pot has a mesh size of 45 mm.

An otter trawl consists of cotton netting with a mesh diameter of 2—4 inches (5.1—10.2 cm), suspended 25—28 feet (7.6—8.5 m) on a multiple line 0.5 inches (12.7 mm) in diameter. The boards used in the rigging of a trawl usually weigh 250 pounds (118 kg), each measuring 3 x 5.5 ft (0.9 x 1.7 m). Scare chains hung across the opening are also used here. These types of otter trawls and beamtrawls with a mesh size of 50—100 mm are used to harvest the scallop off the coast of Western Australia (Record catch..., 1984).

The Atlantic species of the scallop are caught mainly from trawlers more than 50 ft (15.2 m) long and equipped with dredges, as well as by fishing and fish-processing vessels over 80 ft (24.4 m) in length; the latter provides complete or partial processing of the catch. However, small 35-ft (10.7 m) vessels are usually used (Broom, 1976).

When searching for and mapping scallop stocks, one should first select the coastal areas, bays, etc. where the scallop is likely to be found, i.e. areas with the most suitable conditions for the mollusks (suitable substrates, currents, depths, temperatures, salinities, etc.). Then, a system of stations covering the entire water area is projected. This is followed by trawling or dredging operations. The scouting procedure is described in greater detail in Skalkin's "Biology and Harvesting of the Yezo Scallop" (Skalkin, 1966).

With the introduction of underwater photo- and video cameras, as well as manned and unmanned submersibles, the scouting possibilities have increased considerably, not only with regard to mollusks, but other marketable invertebrates as well.

18.3. Protection and control of the scallop industry

At the end of the 19th century, a special permit was required in Primorye for the right to harvest the scallop, though the local population freely harvested mollusks for their own use (Razin, 1934).

In many states of the USA, a law was introduced to limit the scallop catch, productive capacity, and the number of individuals involved in the scallop trade. For example, not more than 10 bushels (3.5 hectolitres), including the shell, are allowed to be harvested per person during the scallop season in the state of Massachusetts. In the state of Maine, licenses are issued to those who wish to harvest the scallop for commercial purposes. Non-licensed harvesting is also allowed, but only in quantities not exceeding 2 bushels (0.7

hectolitres) of scallop in the shell, or not more than 3.8 litres of shelled scallop per day. There are also restrictions on productive capacity; in the state of Maine, for example, dredging for the scallop is limited to the use of a combination of dredges not more than 8 ft (2.44 m) in width, whereas in the Washington area, the width of the dredges must not exceed 4 ft (1.22 m).

In order to protect the young, different states have also set a minimum air temperature level (-3.9°C) for the harvesting of the scallop, since juveniles can freeze when hauled aboard. Restrictions have also been set on harvesting time in order to protect the spawning portion of the scallop populations. A minimum size limit has also been established for the scallop, a shell height of not less than 2.25 inches (57.15 mm) in the state of New York, 3 inches (76.2 mm) in the state of Maine, etc. The rules allow for the presence of a certain proportion of juveniles in the landings, 2% in the state of New York, 5% in Massachusetts, 10% in Maine (Broom, 1976).

In Japan, poaching resulted in the downfall of the scallop industry, almost to the point of extinction. As a result, fishery cooperatives headed by scientific establishments began to be established in 1952; these undertook measures aimed at the conservation of the Yezo scallop stocks. The harvesting season was shortened, a size limit was set (not smaller than 8 cm), the annual rate of exploitation (even the rate per vessel) was established, control of the scallop's natural enemies (starfish) was stepped up (each vessel had to bring in 3750 kg of starfish per season), and the release and planting of juveniles gathered in a natural environment were carried out (Martinsen, Sadykhova, 1966).

In the USSR, the country's first sea sanctuary was established in Peter the Great Gulf in 1978 to protect the natural populations of marine animals, including the Yezo scallop.

At the present time, one of the major goals in the management of the oceans' resources is not so much to increase the exploitation of commercially important marine organisms, as to control the catch and to search for ways of increasing the natural production of the seas and oceans. The expansion and intensification of uncontrolled exploitation in some cases leads to excessive exploitation of the major commercial species and a decrease in their biotic potential, after which further exploitation becomes unprofitable. Because of this, it has become necessary to establish controlled underwater plantations for breeding and raising marine organisms.

In the Soviet Far East, Posyet Bay has been found to be the most convenient for the breeding of scallops and oysters. A special expedition of the USSR Academy of Sciences Zoological Institute and the Pacific Ocean Scientific Research Institute of Fisheries and Oceanography of the USSR Ministry of the Fishing Industry, headed by A.N. Golikov and O.A. Skarlato, worked in this area from 1962 to 1966. The expedition studied the composition, structure and distribution of the biocoenoses of the upper, most productive, zones of Posyet Bay (Skarlato et al., 1967; Golikov, Skarlato, 1969). The biological premises for organizing controlled underwater mollusk plantations in this bay were developed.

18.4. Utilization and processing

The adductor muscle and the mantle are the most nutritious parts of the scallop. The proteins of scallop meat contain all the amino acids required by the human body. The content of these proteins in scallop is higher than in fish. The adductor muscle of the scallop is particularly rich in nitrogenous substances and carbohydrates. The meat of this mollusk is a valuable source of minerals such as sodium, potassium, calcium, magnesium, sulphur, phosphorus, iron, iodine, etc.; it also contains traces of strontium, barium, cobalt, lithium and arsenic, as well as vitamins B_1, B_2, B_6 and B_{12}. The lipids contain sterols, from which vitamin D is synthesized in the human body.

Though the meat of the mantle is less nutritious than the muscle (it contains more water and almost half the amount of protein), it has a higher content of minerals. This is due to the fact that numerous glands which secrete building material for the shells are concentrated in the tissues of the mantle.

Dried and ground, the valves of the mollusk can be used as a mineral supplement for birds. The inedible parts of the scallop's body are used in the production of feed meal. Local industrial enterprises use the shells of the Yezo scallop to make souvenirs, ashtrays, buttons and various other ornaments. The valves of the scallop are extensively used at maricultural establishments to make collectors for the larvae to settle on.

The meat of the mantle and muscle are excellent food products (both as intermediate products, and various canned foods). Several kinds of canned products made from scallop and other sea produce are put out by Soviet enterprises.

Scallop meat in its own juice. Cooked adductor muscle is used for this. Prior to canning, the muscle is marinated in a salt solution, sterilized at a certain temperature, and quickly cooled. The ready canned product contains 60—65% meat and 35—40% broth.

Scallop meat with rice. The muscle and mantle are passed through a meat grinder. Ground spices and taste enhancers, black pepper and pimento, nutmeg, clove, vegetable oil, and chopped and fried cooking onions are added to the ground meat. Dry rice is soaked in boiling water; after it swells and the excess water is drained, it is mixed with the meat. The mixture is sterilized in cans which are then quickly cooled.

Scallop pilau. Cooked muscle and mantle meat is dredged in flour and fried in vegetable oil; the rice is cooked, drained of excess water and mixed with fried onion and spices. The mixture (60% meat, 40% rice) is sterilized in cans which are then cooled.

Assorted seafood. The roe, milt roe, muscle and mantle of the Yezo scallop, all properly processed, are placed in cans, covered with a mixture of sea cabbage and carrots, and then smothered in tomato sauce. The sauce is prepared from tomato paste, salt, sugar, onion, vegetable oil, spices and vinegar. Mustard and dill sauce give meat marinated beforehand in a salt solution a delicious aroma.

The meat of the Yezo scallop is also sold freshly frozen; to prepare in domestic conditions, it should be thawed at room temperature, then washed thoroughly in cold water. Scallop meat can be eaten either raw or cooked. To cook, the prepared meat is placed in salted boiling water (1—2 teaspoons of salt per litre of water) to which pepper, carrots, parsley or celery have been added, and cooked for 3—10 min. This method of cooking almost completely preserves the high taste qualities of the meat. After ccoling, the meat is separated into fibres, or cut into whatever form required for the dish being prepared. The broth can be used for soups.

Those interested in recipes for scallop and other seafood dishes (squid, echinoderms, crustaceans) can refer to O. Selyuk and M. Shadrin's book "200 Seafood Dishes" (Vladivostok, 1969) and O. Selyuk and Ye. Nasedkina's "Poisedon's Gifts" Vladivostok, 1984).

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Fig. 1. Yezo scallop

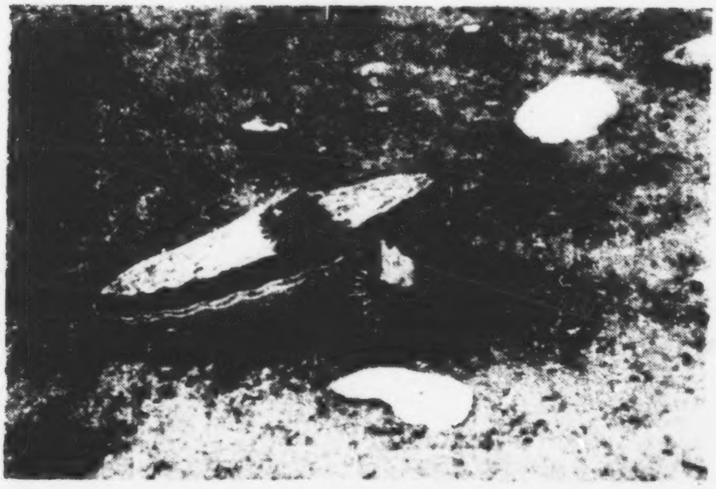

Fig. 4. Community of Yezo scallops and sea-urchins at a depth of 25 m off Furuhelm Is.

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